The impact of grazing along an environmental gradient in the Kamiesberg, South Africa

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ABSTRACT

The Kamiesberg Mountain range, which is situated within the arid Succulent Karoo biome, South Africa, is internationally-recognised for its high conservation value and forms the study site for this project. The Kamiesberg is straddled by the Leliefontein communal area, which has been stocked for many years at twice the rate of the adjacent private rangelands. This presents an opportunity to test whether and how high stock numbers impact on vegetation. In the literature the drivers of rangeland ecology are discussed predominantly in the context of the equilibrium versus non-equilibrium debate, where density-dependent or climatic factors influence the vegetation respectively. Recent dissatisfaction with these paradigms has lead to the exploration of models better placed to incorporate the complex dynamics of rangelands.

Plant cover and community data, as well as abiotic data, were collected in a series of modified Whittaker plots, paired on either side of the communal and private rangeland boundary. Data was collected in six different vegetation types across the entire mountain range, with consideration to lowland and upland habitats. Firstly, data from the less heavily-grazed private rangeland was used to characterise the vegetation and understand abiotic determinants of plant communities sampled across the Kamiesberg. This examination broadly denotes three ecoregions based on climatic and soil drivers, namely a western, upper and eastern ecoregion. A topographical mask of lowland and upland habitats adds to the diversity of the area.

Next, data from the across the communal and private boundary was contrasted in a series of studies which explored the impact of grazing on key vegetation parameters. The impact of heavy grazing on plant growth forms and on standing perennial biomass demonstrated significant shifts in plant composition with losses in cover and biomass of palatable perennial woody shrubs and an increase in herbaceous cover, mostly annuals, on the communal lowlands. A plant functional type analysis indicated that more xeric vegetation types intrude into more mesic areas on heavily-grazed communal rangelands. These findings all point to a degraded system on the communal rangelands where vegetation dynamics are closely tied to rainfall, rendering farmers more vulnerable to drought and to possible future climate change ‘shocks’. A remote sensing study showed close correlations between spectral indices and cover and biomass, but these did not translate into robust thematic maps for the region which differentiated clearly between communal and private rangelands.

While density-dependent effects are evident in this study, the equilibrium and non-equilibrium paradigm does not provide a suitable theoretical framework for this study. The conclusions highlight the need to reduce grazing pressure on communal rangelands so that associated conservation and livelihood concerns can be addressed. In this regard, the importance of strong institutions to manage interventions, and the need for more cooperative work between scientific and social communities is critical.

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CONTENTS

1. INTRODUCTION

1.1 THEORETICAL CONTEXT: ISSUES AND DEBATES IN THE LITERATURE

The aim of this study is to establish whether, and if so how, the sustained heavy grazing associated with the Leliefontein communal rangeland in Namaqualand impacts the vegetation of the area. This essentially involves two tasks. The first is to develop a detailed understanding of the vegetation of the area, and the second is to examine the effects of sustained heavy grazing.

1.1.1 Characterising vegetation

The Leliefontein communal rangeland, situated in the desert of Namaqualand in the Succulent Karoo biome, straddles the Kamiesberg mountain range and is home to diverse and varied plant communities. The desire to understand the workings of these plant communities; who gets to neighbour whom, and what determines plant community boundaries, is fundamental to the science of botany. The following quote from Whittaker (Whittaker, 1978b) captures this fascination.

> *Over the land surface of the world there extends a mantle of vegetation, a living fabric of plant communities that is diverse and subtle in its response to the environment, varied in its structure and composition, expressive of the biological productivity of the land, and interesting and aesthetically appealing....*

Aside from mapping efforts (Mucina and Rutherford, 2006) and numerous localised studies, no attempt has been made to present a detailed characterisation of the dominant vegetation types of the whole Kamiesberg area since Adamson's work in 1938 (Adamson, 1938). This study, which also covers a wider area than Adamson's survey, takes this characterisation one step further by exploring system drivers. This study also acknowledges the importance of species interactions and in acknowledging that vegetation itself can impose disjunctions, some thought is also given to the potential role of plant competition in interpreting results (Beals, 1969; Austin et al., 1984).

1.1.2 Grazing studies: the equilibrium versus non-equilibrium debate

Once the vegetation is characterised, the second task is to look at the effects of sustained heavy grazing on the vegetation of the area. The ecological mechanisms associated with livestock grazing in arid and semi-arid areas such as Namaqualand, and in particular on communal rangelands, have a long history of enquiry (Vetter, 2005). Originally, rangeland ecology was assumed to follow a classic Clementsian succession model where plant community composition succeeds in a linear trajectory from a pioneer stage to a climax or equilibrium stage (Ellis and Swift, 1988; Hoffman, 1988; Ellis et al., 1993; Campbell et al., 2006). This theory had its origins in the balance-of-nature concept, hinged primarily on Malthus's theorem, developed in the late 1700s, that all populations are food-limited and that a density-dependent relationship keeps populations in equilibrium (Ellis et al., 1993). Any interference, such as grazing in rangeland ecology, will retard the course of this linear process. In this model, which became known as the equilibrium model, animal numbers are viewed as tightly coupled to vegetation, and where high animal numbers will have a negative impact on the vegetation of the rangeland (Ellis et al., 1993; Scoones, 1995; Vetter, 2005; Campbell et al., 2006). Consequently equilibrium systems are viewed as stable, and potentially destabilised through heavy grazing as a result of overstocking (Ellis and Swift, 1988). Proponents of the equilibrium model see the potential outcome of heavy grazing as land degradation (Vetter, 2005; Campbell et al., 2006). On the basis of the equilibrium model, a conservative stocking strategy is adopted, where livestock numbers are kept at a level where the carrying capacity of the rangeland is unlikely to be exceeded in dry years (Campbell et al., 2006). Livestock carrying capacity is a simple extrapolation of the density-dependent function where forage consumption equals forage production, populations cease to grow as they are limited by forage supply, and death rates and birth rates are stable (Behnke et al., 1993). The equilibrium model has formed the basis of most grazing policies over the last century (Hoffman and Ashwell, 2001), where the notions of density dependence and range monitoring have informed prescribed carrying capacities (Vetter, 2005).

In the 1980s there was growing concern over the livelihoods of communal pastoralists and, in combination with an increasing dissatisfaction with the balance-of-nature notion in science in general, existing grazing policies were bought under scrutiny (Ellis et al., 1993; Oba et al., 2000; Vetter, 2005). There was concern that grazing policies, founded in the equilibrium model, were based on social assumptions such as Hardin's *Tragedy of the commons* where private gain overrides private cost which is carried by the community (Hardin, 1968), and over-simplified ecological theory where overgrazing is an assumed outcome of high stocking numbers (Oba et al., 2000; Vetter, 2005). The finer complexities of common property as opposed to open access, and emerging ecological theories of chaos and complexity challenged the theories on which the historical grazing policies were based (Ellis et al., 1993; Chesson et al., 2004). Following this debate, a 'new rangeland ecology' emerged in the 1990s which proposed that rainfall is such a significant and dominant factor in arid and semi-arid systems that livestock numbers are always maintained below a level where they might impact the vegetation of the range (Ellis and Swift, 1988; Scoones, 1995; Vetter, 2005; Campbell et al., 2006; Gillson and Hoffman, 2007). This model, which was termed the non-equilibrium model by Wiens (Wiens, 1984), was supported at the outset by extensive work over nine years in Kenya (Ellis and Swift, 1988). An important feature of this work in the Turkana district in Kenya, where rainfall is between 300 – 400 mm per year, was the demonstration of the significance of opportunistic movement, where herders could move livestock in pursuit of forage (Ellis and Swift, 1988; Behnke and Scoones, 1993). On the basis of the non-equilibrium model a more opportunistic stocking strategy is recommended (Campbell et al., 2006). In this instance stock numbers can be increased or decreased according to available forage, thus 'tracking' the spatially and temporally diverse productivity of the rangeland (Campbell et al., 2006). Non-equilibrium systems are not viewed as stable, but rather as being in a constant state of flux. However, they are considered persistent in the face of heavy grazing (Ellis and Swift, 1988).

A debate ensued with two polarised views; the older equilibrium model where biotic interactions were viewed as the primary driver, in opposition to the more recent non-equilibrium model where abiotic forces were purported as sufficiently major to negate

any suggested grazing related density-dependent feedback. Some parties felt the more conservative equilibrium model gave a lower risk strategy for pastoralists with less chance of degradation to the natural resources on which they depend. Density-dependence effects have been clearly demonstrated in numerous rangeland systems with evidence of reduced productivity (Coppock, 1993; Fynn and O'Connor, 2000; Vetter, 2003; Archer, 2004; Zhao et al., 2005), composition shifts (Beeskow et al., 1995; Todd and Hoffman, 1999; Riginos and Hoffman, 2003), and altered soil ecosystems (Allsopp, 1999; Vetter, 2003; Zhao et al., 2005). In addition to feeling supported with considerable evidence for density-dependence relationships, proponents of this view also tackle the non-equilibrium model for its lack of mechanistic clarity (Gillson and Hoffman, 2007). On the other hand some systems have been shown to be highly resistant to any form of density-dependent impacts, in particular where high levels of mobility are an option (Ellis and Swift, 1988; Ellis et al., 1993; Scoones, 1993; Tapson, 1993). These studies suggest pastoralism is an effective livelihood that allows people to cope with the high climatic variability that is so characteristic of arid and semi-arid areas (Hesse and Cotula, 2006). Advocates of the non-equilibrium model feel that the imposition of carrying capacities, a function of the equilibrium model, leads to under-utilisation in wet years, which could possibly also lead to deprivation and poverty (Ellis and Swift, 1988). Recent arguments have suggested that an equilibrium model favours conservation concerns at the expense of social justice (Benjaminsen et al., 2006).

While most practitioners now agree that no system is in an entirely stable state of equilibrium (Hoffman, 1988; Walker, 1993; Cowling, 2000; Reynolds et al., 2007; Richardson et al., 2007), and there has been a flurry of new work emerging from this debate in search of a new paradigm for rangeland ecology, there are still divergent views around grazing and density-dependent impacts. An important component of the debate is perception. Recently Hein (Hein and de Ridder, 2006) demonstrated a reduction in rain-use efficiency in the vegetation of a semi-arid rangeland in the Ferlo in Senegal in response to high stocking rates and heavy grazing (Retzer, 2007). Retzer (2007) reinterprets the data set used in this study and presents a non-equilibrium response in the vegetation, refuting Hein's findings. Indeed the same can be said of work in the

communal areas of Namaqualand where one study demonstrated reduced vegetation cover in response to high stocking numbers on the communal rangeland (Todd and Hoffman, 1999), while another attributed these differences rather to vegetation recovery on the private rangeland through de-stocking (Benjaminsen et al., 2006). In light of the apparent role of perception, methods used in these studies must be made explicit.

1.1.3 Grazing studies: rangeland degradation and vulnerability

The notion of degradation, or more simply that prolonged heavy grazing has long-term negative impacts on the forage resource, is at the heart of the debate over the different grazing models. Equilibrium thinkers hold land degradation as a rationale for setting carrying capacities while non-equilibrium thinkers do not believe there is a link between grazing and land degradation (Ellis and Swift, 1988; Scoones, 1993, 1995). Land degradation itself, even among staunch believers in degradation, is a contested term with variable meanings in variable contexts (Gray, 1999; Ash et al., 2001; Reynolds and Stafford Smith, 2001; Gillson and Hoffman, 2007). While the United Nations Convention to Combat Desertification give the largely accepted broad definition of land degradation as 'the reduction or loss of the biological and economic productivity and complexity of terrestrial ecosystems', the finer details of exactly how this translates in the field are still disputed (Reynolds and Stafford Smith, 2001). The inability to agree on a single useful definition of what constitutes land degradation, and therefore how it is measured (Gray, 1999), has further fuelled the debate (Oba and Kotile, 2001). Practitioners following the equilibrium model would look to the state of rangeland vegetation as a measure of degradation, using a definition such as 'a decline in forage production for a given rainfall' (Walker et al., 2001). On the other hand practitioners using a non-equilibrium model, which holds livestock and vegetation uncoupled, would look to livestock numbers to see how pastoralists are faring, following a definition of degradation such as ' the loss of an economic good', in this instance livestock (Behnke and Scoones, 1993). Indeed in a non-equilibrium state where no 'ideal' or climax vegetation can be established, no yard-stick against which to measure change can be generated (Sprugel, 1991). The search for evidence to support the presence of degradation and the mechanisms of change is confounded by uncertainty about how to

distinguish between the two paradigms and in measuring the relative contributions of climate versus grazers (Briske et al., 2003).

While the mechanisms of how degradation occurs and how it might be avoided are still debated in the context of the different paradigms of rangeland ecology, most parties now acknowledge that degradation is a reality in a wide range of arid and semi-arid systems (Reynolds and Stafford Smith, 2001; Vetter, 2005; Reynolds et al., 2007). Recent figures state that 10 – 20% of the worlds arid and semi-arid regions have some degree of degradation and this affects 250 million people (Reynolds et al., 2007). No attempt is made in this study to settle on a definition of degradation, and given the complexity and contested nature of the term, rather the term alteration is used to refer to a negative, long term change in range condition in considering any results obtained (Reynolds and Stafford Smith, 2001; Walker et al., 2001). The term degradation is only used in the context of cited literature. Understanding the scales and causes of alteration is complex, particularly because it is so heterogeneous in nature. In the case of grazing, which is frequently alluded to as the cause of system alteration, the loss of mobility and supplementary feeding are cited as significant contributing factors (Coughenour, 1991; Vetter, 2005).

These altered, or degraded, landscapes leave people vulnerable to poverty (Downing and Ludeke, 2001). Vulnerability is described as a complex, multi-layered social space, where people or households are exposed to external risks, shocks and stresses and are then unable to cope with or recover from the associated impacts, for example in recovering lost or reduced livelihoods (Vogel and Smith, 2001). For people living in arid and semi-arid areas the loss of rangeland productivity is potentially a loss in livelihood and an increase in vulnerability to external shocks (Vogel and Smith, 2001). Climate change, predicted in the Karoo to lead to increased aridity and more extreme climatic events (Rutherford et al., 2000), is likely to increase vulnerability.

1.1.4 Grazing studies: nuances, complexities and emerging paradigms

What is emerging from the equilibrium versus non-equilibrium debate and associated research is that rangeland ecology is more complex than suggested by either model. Some feel there may be value in both, either as two separate paradigms to explain different systems (Ellis et al., 1993), or in integrating them into one model (Briske et al., 2003), while others feel that all the existing models are inadequate to explain rangeland dynamics (Oba et al., 2000; Skarpe, 2000). The diversity of systems suggests that a continuum exists between the equilibrium and non-equilibrium models, and that different rangelands are positioned variably along this continuum (Campbell et al., 2006). Indeed in his original challenge of the equilibrium model and descriptions of non-equilibrium states, Wiens talks of a gradient between the two states (Wiens, 1984). For example, early support of the different models suggests that the equilibrium model holds better in more mesic areas where rainfall is predictable, and the non-equilibrium model in more arid and variable environments (Scoones, 1995; Campbell et al., 2006). In addition to invoking thresholds of aridity and predictability, recent research in rangeland ecology has shown it to be a highly complex science with, in addition to biophysical aspects, social, economic, political and historical facets all of which have an influence on resource use (Campbell et al., 2006). There are a myriad of different factors that feed into the nuances of where along this continuum any one rangeland is positioned (Campbell et al., 2006).

Livestock numbers do matter, and where high concentrations are maintained for sustained periods of time this invariably results in transformed landscapes (Vetter, 2005). However, the matter is far more complex than simple numbers. The reasons for which people keep livestock, the herd size, and how they manage their herd is dictated by an array of issues, and these in turn affect range ecology. Social issues and values, to name a few, vary with cultural beliefs, and may range from family size and the availability of herders, to risk management and recreational pleasure (Baker and Hoffman, 2006; Hesse and Cotula, 2006). Economic aspects include the proximity and availability of markets, discount rates based on current versus realised costs, the diversity of available livelihood options, and additional income sources such as government grants (Campbell et al., 2006). Political issues range from international interventions in the form of aid, national policies around

land tenure and mobility, and the efficacy of local institutions and support (Campbell et al., 2006). Any contemporary behaviour is informed by the past, and this is highly relevant in the South African context where our history has seriously disadvantaged some in favour of others (Hoffman and Rohde, 2007b). Landscape too, the template on which current practices are played out, is also a function of land-use history (Lunt and Spooner, 2005), which will in turn influence practice. Biophysical considerations include the influence of key resource areas. These are areas of high productivity in a landscape, such as riverine areas or better vegetated but more remote upland areas, which maintain livestock numbers through dry periods, and the ratio of these areas to other less productive areas will affect the number of livestock that can be supported by a landscape (Illius and O'Connor, 1999). Another significant biophysical factor in determining range condition is plant abundance and composition prior to being grazed (Augustine et al., 1998; Fynn and O'Connor, 2000). Climatic variability is a major consideration in livestock keeping (Ellis and Swift, 1988; Coughenour, 1991), and in addition to inter-annual and intra-annual as well as spatial variability in rainfall, prolonged drought and temperature have dramatic effects on herd fertility and survival (Todd and Hoffman, 2000; Oba, 2001). While the exact implications of climate change are uncertain, this additional degree of climatic variability will undoubtedly affect rangelands and pastoralists. Climate-related displacement and subsequent conflict among pastoralists has already been reported elsewhere in Africa (Hesse and Cotula, 2006).

In their review of stocking schemes and range management practices, Campbell et al. (2006) conclude that 'one size does not fit all'. While their paper suggests that virtually every system is unique, they do make the important points around context and complexity which must inform all rangeland ecological studies. Gillson and Hoffman (2007) argue for the use of systems theory, which would accommodate the complexity of rangeland systems, and the replacement of the concept of a carrying capacity with that of a 'moving attractor', a point that would vary depending on rainfall and towards which animal numbers might tend (Gillson and Hoffman, 2007). They go on to argue that by engaging with these complex conceptual frameworks we may more readily define controversial terms such as degradation in these highly variable systems. Cowling cautions against the

over-zealous adoption of a non-equilibrium model in generating land use and land reform policies prior to rigorous review (Cowling, 2000). Illius and O'Conner (1999) say that while equilibrium in the strict sense may not apply to rangelands, density-dependence does and any new paradigm for understanding pastoralism in Africa must acknowledge this.

1.1.5 Grazing studies: difficulties in measuring change

Another factor preventing consensus is the means by which these theories are tested and impacts demonstrated. Animal numbers and vegetation change are not easily coupled. The diversity of factors driving rangeland ecology outlined above, such as the provision of supplementary feed or key resource areas, may de-couple range condition and animal numbers, and a system may appear to support higher animal numbers than the apparently depleted range would suggest (Ash et al., 2001; Vetter, 2003; Rohde et al., 2006). Another difficulty is separating out climatic and grazing impacts, where climatic variability is frequently invoked as the cause of change or degradation (Reynolds and Stafford Smith, 2001; Briske et al., 2003). Attempts have been made to address this through removing the effects of rainfall variability in a remote sensing analysis of grazing impacts in the eastern Karoo (Archer, 2004). However, remote sensing studies do not always provide an accurate representation of conditions on the ground (Chapter 6, this thesis). Some practitioners do not feel that biodiversity is a relevant measure when considering forage production and livelihood in looking at cause and effect and care must be taken in linking appropriate measures (Reynolds and Stafford Smith, 2001). There has also been a growing sense that numerous small-scale local studies, using variable methods do not allow for global comparisons or make contributions to a universal understanding of mechanisms and responses (Rutherford et al., 1995; Landsberg et al., 1999). These issues around measuring grazing impacts remain a challenge to rangeland ecology.

1.1.6 Grazing studies: ecosystem functioning, conservation and grazing

Ecosystem services are the benefits provided by ecosystems to humans, such as the provision of clean water (Diaz et al., 2006). There is compelling evidence that the loss of

biodiversity, be it in species or functional diversity, affects ecosystem functioning and therefore human well-being (Diaz et al., 2006). The conversion of land for crops, grazing and cities is an integral element of human existence (DeFries et al., 2004), and currently land use change for growing agricultural demands is cited as possibly the worst threat to global biodiversity (Dorrough et al., 2004a). So while the conversion of land provides essential ecosystem services, accessing these services simultaneously alters functioning, with negative effects on the provision of a range of other ecosystem services.

In some ecosystems grazing has been shown to alter plant composition and diversity with knock-on effects for other assemblages such as bird and invertebrate communities and soil health (Allsopp, 1999; Joubert and Ryan, 1999; Seymour and Dean, 1999; Ayyad, 2003). Issues of biodiversity conservation in relation to grazing impacts are also gaining momentum. This is particularly true of the Kamiesberg which is situated in a biodiversity hotspot and has been described as an area of noted biodiversity and conservation concern (Hilton-Taylor and Le Roux, 1989; Lombard et al., 1999; Mittermeier et al., 2004).

Concern around the preservation of the plant and animal diversity of the world's arid and semi-arid ecosystems generates increased controversy in a research area already fraught with conflict. Some feel that the conservation lobby and natural scientists hold on to the notion of carrying capacities to meet their own interests in preserving diversity based on value systems in opposition to the livelihoods of the rural poor (Benjaminsen et al., 2006). However, rural people living in these areas are dependent on the natural resources and are also essentially interested in the maintenance of their resource base (Hesse and Cotula, 2006). Conservation policies in South Africa have started to engage with local communities and have begun to adopt community-based approaches (Benjaminsen et al., 2006). The translation of this into practice though, often in association with ecotourism and in ways that constrain people's livelihood choices, means conservation has remained a contested issue between the desires of authorities and those living on the land on which conservation ends are sought (Boonzaier, 1996).

Land use decision-makers have the difficult task of finding the balance between satisfying human demands and the unintended repercussions to ecosystems, while meeting the values of society as a whole (DeFries et al., 2004). In rangeland ecology this translates into a need to develop management strategies that simultaneously meet conservation and agricultural needs (Dorrough et al., 2007). New models and a number of suggested mechanisms are emerging, such as intensification of land use in productive areas or the identification and correction of key imbalances (Bernues et al., 2005; Dorrough et al., 2007; Lunt et al., 2007). There is a sense of hope and opportunity that there are some exciting and viable solutions beyond the traditional exclusionary or livelihood constraining conservation practices (Blignaut and Loxon, 2006). From these emerging research areas there is a call for more information about how systems function so that informed decisions can be made (Ayyad, 2003; Dorrough et al., 2004a).

1.2 RATIONALE AND CONTEXT FOR THIS STUDY

Arid and semi-arid lands, home to one billion people, account for 40% of the earths land surface, and of this area 88% is managed as rangelands (Reynolds et al., 2007). In South Africa more than 80% of the natural vegetation is under management for livestock production (du Toit et al., 1991). Grazing by domestic livestock is cited as the most important disturbance in terms of loss of plant biomass after fire (Diaz et al., 2007). Excessive loss of vegetation, or loss of useful vegetation, and in turn potential degradation, can negatively affect the livelihoods of the vast numbers of people who live on these arid and semi-arid rangelands and depend on these natural resources (Veron et al., 2006). Subsistence and rural farmers are the most dependent on ecosystem services. In South Africa, even where government grants play a major role in the economies of the rural poor, the land has been shown to be a highly significant element in supporting rural livelihoods (Shackleton et al., 2001). The consequences of the loss of ecosystem services will be felt most by this group, further increasing existing inequalities (Scherr, 2000; Diaz et al., 2006). Land degradation can cause or exacerbate vulnerability (Downing and Ludeke, 2001). Those studying degradation appeal to scientists for more work exposing

possible future degradation in order that it may be anticipated and suitable interventions put in place to avert negative social consequences (Vogel and Smith, 2001). The Kamiesberg area is of considerable conservation significance (Hilton-Taylor and Le Roux, 1989; Lombard et al., 1999; Mittermeier et al., 2004) and a detailed understanding of this resource as undertaken in this study is easily justified from the standpoint of both livelihoods and conservation.

A better understanding of the functioning of grazing systems is called for in numerous studies (Ayyad, 2003; Dorrough et al., 2004a). There is a need for more detailed studies, for example, in the identification of those aspects of the landscape that are more susceptible to grazing impacts than others (Vetter, 2005). By including the dimension of the characteristic upland and lowland habitats of the Kamiesberg, this study will also give some insight into the response of these smaller-scale landscape elements to sustained heavy grazing. Another gap identified in the literature is that of larger scale studies. Frequently grazing studies are extremely local in nature, where little can be gained in understanding general responses beyond the immediate ecosystem. At the centre of this current study is an examination of grazing related impacts across a diversity of vegetation types, which are a function of different abiotic conditions, increasing the scale of what is currently a localised understanding of grazing impacts in the areas (Allsopp, 1999; Todd and Hoffman, 1999; Petersen et al., 2004).

Another problem facing the measurement of change is the lack of reference points against which to contrast potentially altered systems. This is described as one of the challenges facing degradation studies and there is an appeal for the detailed characterisation of systems to a level where they might be used for future comparisons and to form the basis of projections or modelling exercises (Birch et al., 1999; Fernandez et al., 2001; Veron et al., 2006). Of major significance in terms of justifying this current study, is that research should inform policy, and reliable quantitative knowledge, about ecological processes in relation to habitat structure and in turn ecosystem response to land use, is required for making informed management and policy decisions be they for grazing or conservation ends, or ideally both (Stohlgren et al., 1997; DeFries et al., 2004).

In this study, the use of fence-line contrast sites immediately adjacent to one another, dividing two historically different stocking systems, rules out climate variability due to the immediacy of the paired sites. While the two farming approaches and motivations on either side of the fence are very different, and the nuances of the different systems are acknowledged but not addressed in this study, the consistently different stocking rates over the last 50 years can test density-related impacts. In an attempt to arrive at more universally meaningful measures, this study includes, in addition to measures of biodiversity and composition, a biomass assessment. This aspect focuses on year-round perennial biomass as a representation of forage, the most important ecosystem service to pastoralists. A plant functional type analysis is carried out using a recently proposed universal approach (Corelissen et al., 2003) which has been devised in an attempt to improve global comparisons (Chapter 4). Remote sensing has become an important tool in vegetation assessments and monitoring (Hobbs, 1989; Shupe and March, 2004). In this study the application of a remote sensing approach is tested in its ability to produce thematic maps that accurately reflect what is present on the ground. Approaching one data set with an array of methodologies provides an opportunity to test the value of some of the different approaches suggested in the literature. In each instance the value of these different methods is given due consideration.

In keeping with the sentiment of Whittaker (1978a) in his desire to go out and explore and understand the vegetation of the earth, there is an element within any scientific study that is justified by the pure joy of the pursuit of science. As Kelvin put it, 'to measure is to know' (Smith, 1989). This is a large motivation for this study, to look at the 'mantle of vegetation' and to try and understand its workings, and in turn how our species is affecting the system (Whittaker, 1978a). While this study takes a clearly botanical view, the above literature is presented as it is seen as important to contextualise the findings in acknowledging the multifaceted nature of rangeland ecology. This study does not attribute causes beyond those tested in each study, or in anyway apportion blame. The author is acutely aware of the complexity of the systems at play and hopes that this work

will be a contribution to the growing understanding of the workings of rangeland ecology.

1.3 OBJECTIVES OF THE STUDY AND KEY QUESTIONS

The central aim of this study, to characterise the vegetation of the Kamiesberg region and to examine the impact of grazing, is broadly outlined in the context of the literature reviewed above. The main objectives, to meet this central aim, are as follows.

- To describe the different vegetation types sampled in this study and their association with the Kamiesberg and immediate surrounding area, with particular consideration of the upland and lowland habitats of each vegetation type.
- To develop an understanding of what drives the turn-over in species composition between each of the different vegetation types, and the upland and lowland habitats.
- To look for grazing-related impacts using:
  - a simple growth-form analysis,
  - a plant functional type analysis using an internationally recommended approach in an attempt to foster global comparisons,
  - a standing perennial biomass analysis, and
  - a remote sensing analysis.

  And to carry these out across all the different vegetation types, with consideration of the upland and lowland habitats. This is accomplished by contrasting the vegetation on either side of the communal and private rangeland boundary.
- To consider the value of each of the methodologies adopted.
- To comment on the findings of this study in the context of the current literature and with consideration to recommendations and future research directions.

1.4 GENERAL APPROACH, RESEARCH DESIGN AND LIMITATIONS

In this project I used field surveys, analysed soil samples, and carried out field-based transplant experiments. A Landsat7 image was used to capture spectral data and to generate indices. Climate data was obtained from the South African Atlas of Agrohydrology and Climatology (Schultze, 1997).

The time-scale of the study did not allow for any temporal comparisons. This unavoidable constraint limits the potential to look at trajectories or reversibility of any measured change. Such issues are frequently raised as limitations in the literature (Walker et al., 2001). Comfort is taken in that this study sits among a greater body of work carried out in the area over the last ten years (Allsopp, 1999; Todd and Hoffman, 1999; Riginos and Hoffman, 2003; Petersen et al., 2004) which allows for some temporal consideration, and that this work, which covers a greater area than past work, might serve as a reference point against which future work might be compared. The timeframe of the study coincided with several years of low rainfall and as a result the full complement of the floral diversity was never captured as few annual species germinated in the years in which field work was carried out. While the effect of this temporal limitation was a disappointment to the researcher, it only reflects an important state of the ecosystem under consideration and cannot therefore be considered a true limitation to the study.

1.5 OUTLINE OF THE THESIS

Chapter 1 introduces the project, provides the theoretical context and an overview of the historical debates in the literature. This chapter also presents the overarching aims of the study and the finer-scale objectives to meet these aims, as well as the general approach adopted and limitations. Chapter 2 is an introduction to the study site, the Kamiesberg area, with biophysical, socio-economic and historical background information.

Chapter 3 provides a detailed biophysical characterization of the different vegetation types sampled across the Kamiesberg. Each of the six vegetation types covered in the study site is described with consideration to composition, cover, structure, and growth form, and the abiotic drivers of turnover and change between each vegetation type. Particular attention is given to the upland and lowland habitats in each vegetation type, a feature which are characteristic of the area.

Following on from Chapter 3, Chapters 4 to 7 examine the impacts of the sustained heavy grazing on plant communities associated with upland and lowland habitats in the Leliefontein communal area of the Kamiesberg. Each of these chapters uses a different methodological approach to contrast the vegetation growing across the communal and private rangeland boundary. In chapter 4 a basic growth form approach is adopted. In chapter 5 a plant functional type approach, based on international guidelines and generated in an attempt to standardise this methodology, is adopted. This method groups plants into functional types and these types are then examined for change under the two different land uses. This includes a biogeographic analysis of the distribution of the different plant functional types. In chapter 6 standing perennial biomass is established for each vegetation type and habitat using a regression-based method. This method involved the establishment of volume-biomass curves for the dominant species at each sample site. This is a less destructive sampling method, and the potential to generalise these volume-biomass relationships by grouping species into growth forms was investigated using analysis of co-variance and homogeneity of slopes. In chapter 7 correlations are explored between spectral values derived from a Landsat 7 image and ground-truthed plant cover and biomass values. Thematic maps for a larger area are generated on the basis of established relationships, and their value in reflecting impacts measured on the ground, are tested. Each of these chapters is presented in publishable article format, and consists of an abstract, an introduction to the particular study undertaken in the chapter, building on the literature review presented in Chapter 1, the methods used, results obtained and a discussion.

The concluding chapter, Chapter 8, provides a general discussion of the findings of the study in the context of the broader theories and historical debates in the literature presented in Chapter 1. Possible applications of this work, with consideration to interventions and future research directions are also presented.

2. STUDY AREA

2.1 INTRODUCTION

This chapter provides an overview of the biophysical, socioeconomic and historical context of the study area.

2.2 BIOPHYSICAL CHARACTERISTICS

2.2.1 Geographical location

The study area is located in central Namaqualand, in South Africa's Northern Cape Province, across the boundary of the Leliefontein communal area and the immediately adjacent privately owned farms (Figure 2.1). Namaqualand was formerly a magisterial district. The name has been retained and is used today only in reference to the biogeographic region, a subset of the Succulent Karoo biome characterised by winter rainfall (Cowling et al., 1999b). The Leliefontein communal area is 191 809 hectares in extent and lies in a west-east band straddling the Kamiesberg mountain range from 30º00′00″ to 30º30′37″ S and 17º30′37″ to 18º15′22″ E. The Leliefontein communal area comprises nine villages, of which the village of Leliefontein is the oldest and most central. The communal area extends from the coastal plains in the west, from altitudes of about 300 m. It includes the Kamiesberg mountain (hereafter referred to as the Kamiesberg), which forms the central part of the study area. The Kamiesberg rises to altitudes of around 1400 m, and extends across to the western extreme of the Bushmanland escarpment. This is an adjacent biogeographic region in the east which lies at an altitude of about 900 m.

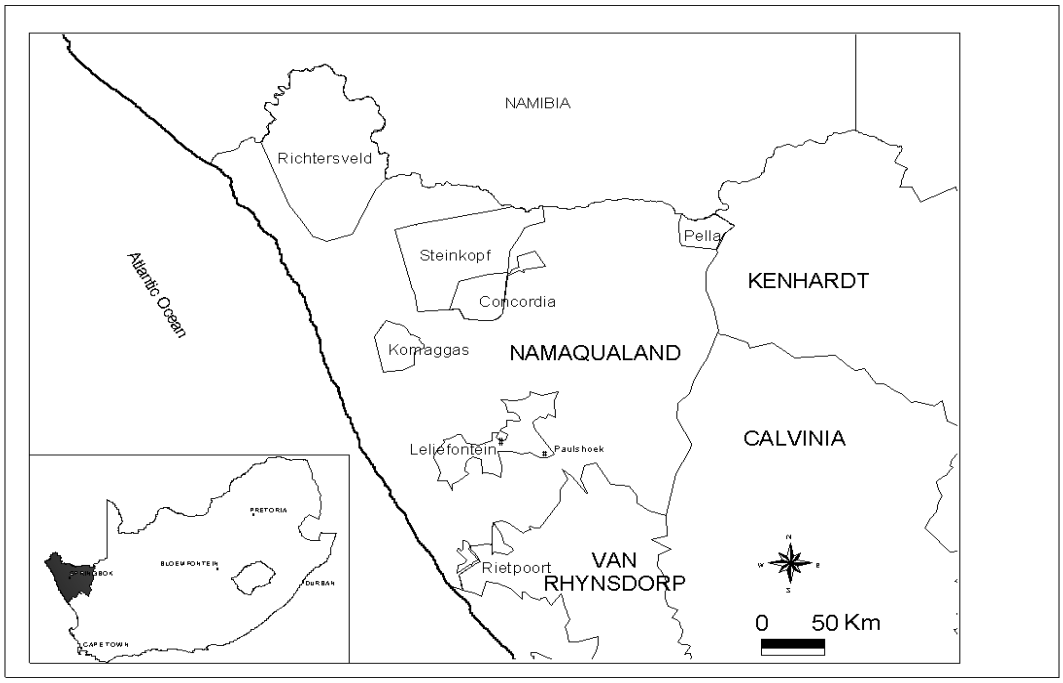


Figure 2.1 Namaqualand with the communal areas shown as 'islands' surrounded by privately owned farms. The study was conducted in and around the Leliefontein communal area. Adjacent districts of Kenhardt, Calvinia, and Van Rhynsdorp are also shown, with the national border with Nambia to the north.

2.2.2 Topography and geology

Following the break up of Gondwana around 90 million years BP, southern Africa experienced a long period of erosion during the Cretaceous period, which resulted in a combination of eroded landscapes and locally preserved uplands (Partridge, 1997). The end of this period, some 65 million years ago, saw the formation of the great escarpment, which tracks the horse-shoe shape of the subcontinent, and leads to the interior plateau. The study area is located on the western rim of the great escarpment, and straddles the coastal margin and the elevated inland plateau. The underlying geology of the area is termed the Namaqualand Metamorphic Complex which comprises a combination of metamorphosed sedimentary rock and volcanic and intrusive rocks, predominantly of granitic gneisses (Watkeys, 1999). The Kamiesberg is characterised by these massive gneiss intrusions in various stages of erosion set among sedimentary plains. This results in a patchwork of rocky upland and sandy lowland areas (Adamson, 1938). To the

western and eastern extremes of the study site these intrusions diminish in frequency and the sandy lowland areas predominate.

2.2.3 Soils

The granitic parent material of the area gives rise to red and yellow colluvial soils which are described as apedal (Watkeys, 1999). The A-horizon is commonly orthic, lacking in organic matter, and the soils are well drained. A gradient runs from west to east of very sandy soils in the west, where proximity to the coastal forelands means these soils contain more aeolian sands, to simply sandy soils in the east (Watkeys, 1999; Francis et al., 2007). The rocky upland slopes, which are more dominant in the centre of the Kamiesberg, are characterised by large boulders and coarse cobbles with shallow lithosols (Francis et al., 2007). To the east of the Kamiesberg these lithosols are increasingly interspersed with older red soils on dorbank (Francis et al., 2007). The granite gneiss parent material generally gives rise to soils with lower concentrations of potassium, calcium, magnesium, copper and zinc than surrounding soils (Watkeys, 1999). In arid regions, parent material and soils are subject to less weathering and leaching and soil formation is slow. These pedologically young soils are, therefore, very similar to their parent material as there is little redistribution of elements during soil formation (Watkeys, 1999; Francis et al., 2007). As a result soils are relatively shallow and coarse and soil boundaries are often abrupt. These attributes render these soils sensitive to degradation (Watkeys, 1999).

2.2.4 Climate

Rainfall and temperature data, from the Computing Centre for Water Research (CCWR) and derived from interpolated covers suggest that rainfall varies considerably across the study site in volume, season and reliability (Figure 2.2). Included in the rainfall figure is ten-year average rainfall data from Paulshoek, a village to the east of the Kamiesberg. Rainfall figures from this eastern extreme demonstrate the influence of the intrusion of summer rainfall, in January and February, to the east of the Kamiesberg. Climate in the area is a function of the influence of two different climatic systems and variable topography and altitude. The bulk of the study site falls within the winter-rainfall regime,

where westerly fronts bring rain to the area during the months of June to August (Desmet and Cowling, 1999b). While aridity is pronounced at the western extreme of the study site, rainfall is most reliable here and is 1.15 times more predictable than the adjacent summer rainfall area to the east (Milton et al., 1997; Desmet and Cowling, 1999b). The low lying plains to the immediate west of the Kamiesberg receive 135 mm of rain per annum. Though marginal to the true coastal plains, these areas may receive some additional moisture from the regular coastal fogs (Desmet and Cowling, 1999b). With a progression to the east there is a pronounced origraphic effect, and the highest rainfall is experienced at the top of the Kamiesberg, where the village of Leliefontein itself receives 280 mm per annum. For the highest peaks this rises to as much as 350 mm per annum. On the eastern slopes of the Kamiesberg rainfall drops to 185 mm per annum. At the periphery of the winter rainfall region, rainfall drops even further, to about 130 mm per annum. At the eastern end of the study site, with the progression towards Bushmanland, the climate is also influenced by tropical systems which bring rain in the form of thunderstorms during the summer months of December to February. The nature of the rainfall also varies considerably. Winter rainfall events are usually gentle, prolonged and widespread, in contrast to the summer rainfall events which are intense, of short duration and highly localised (Desmet and Cowling, 1999b). The coefficient of variation in rainfall ranges from about 38% at the western extreme, to 35% at the top of the Kamiesberg, to over 39% at the eastern extreme.

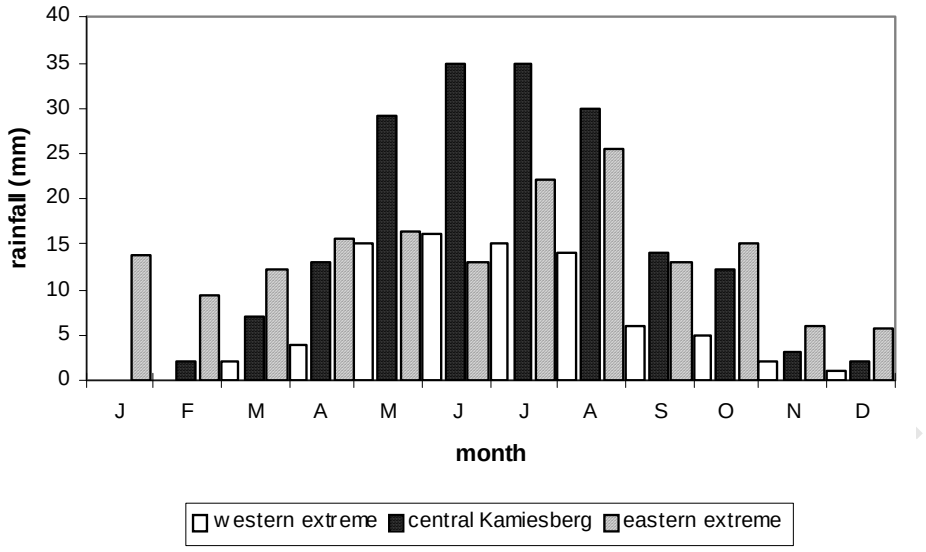


Figure 2.2 Mean monthly precipitation for western, central and eastern points across the study area.

The moderating effect of the Atlantic Ocean is evident at the western extreme of the study site where temperatures range from a maximum of 29º C in January to a minimum of 7 º C in July. These values are about a degree cooler in the summer and a degree warmer in the winter than the immediately adjacent western slopes of the Kamiesberg (Desmet and Cowling, 1999b). With a rise in altitude, seasonal temperatures change fairly uniformly with an average summer maximum of 25º C and winter minimum of 2º C in the vicinity of the village of Leliefontein. While summer maximum temperatures rise with the progression east towards Bushmanland with a January maximum of 30º C, temperature ranges become more extreme and the winter minimum remains at around 3º C. Mean monthly temperatures across the study site are presented in Figure 2.3 below. Frost is extremely rare on the plains to the west of the Kamiesberg and only very occasionally experienced on the western slopes of the mountain. However, at the highest altitude frost days are more common with an average of 32 a year. These taper off to some extent with the progression east, but remain relatively high on the plateau at 19 frost days on average at the extreme east of the study site.

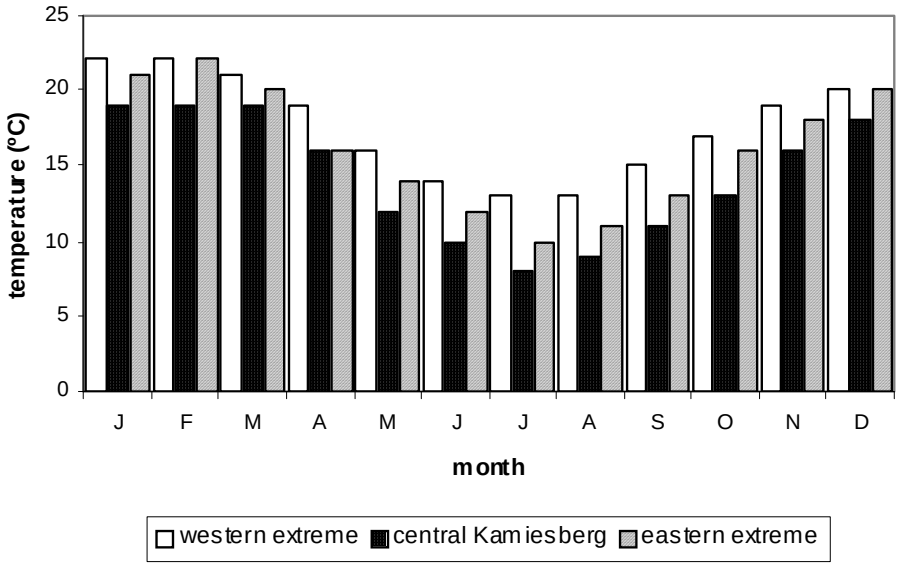


Figure 2.3 Mean monthly temperatures for western, central and eastern points across the study area.

Wind is an important feature of the climatic regime and the west coast experiences predominantly southerly and south-westerly winds arising from steep atmospheric pressure gradients associated with the cold ocean and warmer hinterland (Desmet and Cowling, 1999b). Berg winds, which arise in winter due to inland and coastal pressure differentials, are sometimes experienced on the plains to the west of the Kamiesberg. Inland on the plateau prevailing wind directions are predominantly south-westerly in the summer and northerly in the winter, though winds here are described as more local in nature (Desmet and Cowling, 1999b).

2.2.5 Vegetation

The study area is situated in the Succulent Karoo biome which is one of the smaller of South Africa's seven biomes, accounting for only 100 251 km2 of land (Rutherford, 1997). Despite its limited size, this biome is extremely diverse, with over 6 356 species of which 40% are endemic (Hilton-Taylor, 1996; Desmet, 2007). Recent work in this biome has shown close correlations between plant and small mammal diversity (Keller and Schradin, 2008). The Succulent Karoo is one of only two recognised biodiversity

hotspots in an arid area (Hilton-Taylor, 1996; Mittermeier et al., 2004). The flora of the region is described as unusual when compared to equivalent semi-arid regions around the world due to the scarcity of tall shrubs, trees and grasses and predominance of chamaephytes and geophytes, and its high concentration of leaf-succulent dwarf shrubs (Milton et al., 1997; Cowling and Hilton-Taylor, 1999).

Namaqualand is a region within the Succulent Karoo biome and accounts for a quarter of the area, yet contains some 3 500 species (to the entire biome's approximate 5000), around 25% of which are endemic to the Namaqualand area (Desmet, 2007). This exceptional diversity is not evenly spread throughout Namaqualand, but rather variously distributed thorough a diverse array of vegetation types; the distinctions, distributions and names of which have been described and debated through time (Adamson, 1938; Acocks, 1952; Low and Rebelo, 1996; Mucina and Rutherford, 2004; Desmet and Helme, 2006). The present study only included a small subset of this myriad of vegetation types, and these are discussed in detail in Chapter 3.

2.3 POPULATION AND LAND USE HISTORY

2.3.1 Pre-colonialism

Evidence of human habitation in the western regions of southern Africa stretches as far back as three million years, and the progression through the Early to Middle Stone Age is reflected by shifts in an abundance of stone artefacts from crude hand axes to finer blades and flakes (Smith, 1999). The small stone tools characteristic of true modern people, Homo sapiens sapiens, enter archaeological records in the area some 40 000 years ago in the Later Stone Age (Smith, 1999). These people lived as hunter-gatherers until the first agriculturalists appeared in southern Africa around 2000 years ago (Webley, 2007). An excavation of caves along Namaqualand's coast provides evidence, dating back to 2 100 BP, of a lifestyle of combined hunting and gathering with animal husbandry (Webley, 2007). Excavations of the Bethelsklip cave, situated within the present day Leliefontein

communal area, give the earliest record of domestic goats in Namaqualand, dating back to 800 BP (Smith, 1999; Webley, 2007).

2.3.2 Colonialism

Dutch settlers arrived in the Cape in the mid 1600s and early explorers wrote of two distinct groups of people in Namaqualand; the Bushmen and the Namaqua (Smith, 1999; Webley, 2007). The Namaqua were described as nomadic pastoralists to whom the Kamiesberg, with its higher rainfall and good forage, was pivotal in the transhumance pattern of movement between the winter rainfall Heuweltjieveld (the land to the west of the Kamiesberg of low undulating hills characterised by mima-like mounds) to the west and the summer rainfall Bushmanland grasslands to the east (Lovegrove and Siegfried, 1986; Smith, 1999; Rohde et al., 2003; Hoffman and Rohde, 2007a). In the early 1700s these large groups of Namaqua were severely reduced first by smallpox and in turn, in their weakened state, by repeated attack from the Bushmen (Rohde et al., 2003). By the mid 1700s, as the first European farmers settled in Namaqualand, the Namaqua people were reduced to a state of poverty and adopted a subservient role to the invading settlers.

2.3.3 Formation of Leliefontein as a mission station

Christian missionaries were among the first settlers in Namaqualand. One of these mission stations was established at Leliefontein in 1829, following an agreement between the Namaqua leader Wildschut, and the Wesleyan Missionary Society (Rohde et al., 2003; Hoffman and Rohde, 2007a). This mission station, which gave necessary security and sanctuary to the Namaqua people during these unstable years, became a central point from which they continued to practice transhumance. Stock was moved about between known water points, many of which became the main villages of the present day Leliefontein communal area (Rohde et al., 2003; Hoffman and Rohde, 2007a). There were several instances where churches were appealed to for the protection of traditional grazing lands from invasion and possession by colonists, and these ultimately led to the formation of the original coloured reserves or, what are termed in this study, communal areas (Hoffman and Rohde, 2007a).

2.3.4 Creation of the Leliefontein communal area

In the 1880s the assertion of Common Roman Dutch Law saw the true development of the notion of ownership as exclusive (Wisborg, 2006). After an inconsistent history of governance and ownership, the Leliefontein area was declared a coloured reserve, along with six others in the Namaqualand area, with the enactment of the Communal Reserves Act in 1913, bringing it directly under central government control. This restricted the population to the communal area, and with limited economic opportunities this served to compound the existing poverty (Rohde et al., 2003). In 1940 the Land Settlement Act provided white farmers with grazing licenses that were eventually converted to ownership rights in the adjacent lands and this entrenched the stark division in land ownership. The 1950s Group Areas Act saw the ultimate confinement of coloured people to the communal areas (Wisborg, 2006). This act also resulted in a rise in the population numbers in the communal areas following forced removals from 'white' areas and the simultaneous return of a number of retired people with the provision of pensions. The concurrent fencing of surrounding private lands through the provision of government subsidies brought home the realities of dispossession and exclusion. The differences in fortune were further aggravated as a number of white farmers were able to expand their land to include farms in the summer and winter rainfall regions, while in the communal areas transhumance was restricted to within the communal area boundaries (Rohde et al., 2003).

2.3.5 Tenure systems within the Leliefontein communal area

The system of ownership in the communal areas was one of communal tenure. Provision was made in the laws for the parcelling out of small units to private ownership with the so-called betterment schemes of the 1960s and economic units policy of the 1980s. These attempted shifts away from communal tenure only resulted in further dispossession as most inhabitants faced the loss of both grazing and arable land. Following fierce opposition, the system of 'economic units' was abandoned in 1988 (May and Lahiff, 2007).

2.3.6 The Leliefontein communal area in the young democracy

In the early 1990s, just prior to democratisatifon, 385 white farmers owned 51.8% of the farmland in Namaqualand, while 1650 households of coloured farmers had access to 22.3% of the farmland (May and Lahiff, 2007). Other land ownership and land use in Namaqualand from the same survey includes mining (7.5%), state-owned land (7.3%) and conservation (3.8%), with the remainder comprising the 14 small towns (May and Lahiff, 2007). Following the transition to a democracy in 1994, the government set about a program of land reform to address the colonial and apartheid history of dispossession (May and Lahiff, 2007). Following a proactive process driven by the people of Namaqualand, by 2004, residents of the communal areas had gained access to a further combined 1,897,282 ha of land. This newly acquired land is not managed in the same manner as the older commonage, but through a system of rental to individuals who must then adhere to set stocking rates (May and Lahiff, 2007).

A number of problems have arisen through this model of restitution. Firstly, the matter of the relatively highly-populated and heavily stocked old commonages has not been addressed. A study by May (1997) estimated that an additional 84 240 ha of grazing land would be necessary to relieve the then existing pressure on the Leliefontein commonage, without consideration of the large number of people living on privately owned land or in local towns who should also be included in the land reform programme. To date the Leliefontein communal area has been expanded by only 32 623 additional hectares (May and Lahiff, 2007). Other issues include unequal access, both along gender (Kleinbooi and Lahiff, 2007) and economic lines (Lebert and Rohde, 2007), which remains a problem in the old communal areas and the newly expanded areas. Furthermore, some municipalities are not managing to meet the new financial demands presented by the service requirements of these extended commonages (May and Lahiff, 2007), and payment of grazing licences and the enforcement of stocking rates continue to be erratic (May, 1997; Jonas, 2004; Lebert and Rohde, 2007; May and Lahiff, 2007).

Today the Leliefontein communal area comprises, including the additional new farms, some 191 809 ha, and has a population of 4 825 people, which is approximately 6% of

the total population of Namaqualand (May and Lahiff, 2007). Present day inhabitants are descendants of the indigenous Namaqua and Bushmen, and comprise a range of mix-race communities, that developed with the expansion of the colonial frontier and slaves from east Africa and Asia (May and Lahiff, 2007). Almost all the communities of Namaqualand have a common language in Afrikaans although Nama is still spoken in the northern communal areas. Economic opportunities are limited within the communal areas, and state pensions are a significant income for many households (Rohde et al., 2003). A recent examination of livelihoods in communal areas demonstrates the importance of what is termed 'pluriactivity' where the most successful farmers are those pursuing multiple occupational activities (Anseeuw and Laurent, 2007).

2.3.7 Stock keeping in Namaqualand

Stock keeping boomed in the early to mid 20th century in Namaqualand, until the late 1950s when numbers dropped with the modernisation and commercialisation of agriculture (Hoffman and Rohde, 2007a). This shift reduced the risks associated with stock farming and efforts to stabilise production on privately-owned farms included measures such as controlling stock numbers, managing range, subsidies, and the creation of camps (Hoffman and Rohde, 2007a). From the 1960s onwards, stock numbers were tightly controlled on private farms through government-determined carrying capacities. However, this was not the case for communal areas which were on average stocked at twice the government recommended stocking rates (Hoffman et al., 1999; Hoffman and Ashwell, 2001). Changes in vegetation with the sustained heavy grazing associated with the communal areas has purportedly resulted in greater susceptibility to drought (Todd and Hoffman, 1999; Todd and Hoffman, 2000), and livestock numbers in these areas are seen to fluctuate widely (Hoffman and Rohde, 2007a; Richardson et al., 2007).

Current recommended stocking rates for the Namaqualand area range between 45 and 60 ha per large stock unit (LSU[1]) (May, 1997). Livestock numbers for the Leliefontein communal area, based on surveys by the Surplus People Project (SPP) in 1997 and the

[1] Goat and sheep conversion factors to Large Stock Units = 0.17, cattle = 1.1, and donkeys = 0.65 (Hoffman et al. 1999)

Northern Cape Department of Veterinary Services in 2002, give the stocking rates as 35.5 and 39.5 ha / LSU respectively (May, 1997). The 1997 survey by SPP included a survey of donkey numbers which are in excess of 1000 for the area, which are not included in the previous stocking rate calculations (May, 1997). A recent study shows that over-stocking is by no means restricted to communal areas, but is also recorded on some private farms. While the impact of grazing is recorded on communal areas in contrast to private farms (Todd and Hoffman, 1999), it is possible that the impact on private farms is reduced by some degree of transhumance and historic subsidisation which allowed for supplementary feeds. An additional difference between the two tenure farming practices is that traditionally sheep dominate the private farms while goats are more common on communal lands (Jonas, 2004). Models examining the sustainability and productivity of the pastoral practices on the communal areas corroborate the notion that the communal areas are degraded through extended grazing. They point to continued degradation, little chance of recovery in the short term at current stocking rates and an increase in vulnerability of livestock owners to variable rainfall (Richardson et al., 2007). Communal farmers acknowledge that the communal ranges are overstocked (May, 1997).

2.4 CONSERVATION

The decline in stock numbers in the 1960s coincided with an increase in conservation initiatives in Namaqualand, with increases in vegetation cover and biodiversity on commercial farms and the creation of conservation areas (Hoffman and Rohde, 2007a). The Succulent Karoo currently has four large national parks, of which the Namaqua National Park and the Richtersveld National Park are situated in Namaqualand (van Wyk and Smith, 2001). In Namaqualand the area under formal conservation accounts for only 3.2% of the area (Jonas, 2004). The Succulent Karoo biome is recognised as severely transformed, in particular through grazing (Cowling and Pierce, 1999) and an assessment of future threats from land use include the expansion of communally owned lands and associated overgrazing with possible desertification, mining and the expansion of

croplands (Jonas, 2004). These future land use threats are further compounded by the predicted impacts of climate change (Cowling and Pierce, 1999; Rutherford et al., 2000).

The Succulent Karoo has been identified as the biome most at threat from climate change in South Africa (Rutherford et al., 2000). Projected increases in temperatures pose a threat to a significant number of plant lineages that evolved during cooler times. While rainfall predications are less clear, any drying combined with temperature increases will severely restrict huge numbers of species, dramatically reducing the spatial extent of the biome (Midgley and Thuiller, 2007).

Future land use predictions point to both a decrease in commercial agriculture, with expanding global markets and increases in fuel costs, and a simultaneous expansion of the communal rangelands (Hoffman and Rohde, 2007a). While this de-agrarianization and increases in tourism are considered beneficial to the biodiversity of Namaqualand, the expansion of communal areas is described as a potential threat (Jonas, 2004).

2.5 THE KAMIESBERG IN CONTEXT

The Kamiesberg, which forms the central focus of this study, is a unique biophysical feature situated in an exceptionally diverse biome and is recognised as an area of high conservation priority. No part of it is currently conserved, but there have been several calls for its inclusion is some formal conservation plan (Helme, 1992; Desmet, 1999; Lombard et al., 1999; Desmet and Helme, 2006). However, it is also noted that the landscape diversity of the region is such that no formal conservation network will fully capture the wealth of the region's biodiversity and efforts must be made to incorporate conservation concerns within current land use practices (Desmet, 1999).

The Kamiesberg is less unique in its socio-political history, where it became one of a few small pieces of land allocated to coloured people through a series of policies which bought about starkly different fortunes with regards to matters such as access to land,

security of tenure, and government support. These policies and land use practices have resulted in locally-measurable changes to the biota (Hoffman et al., 2003). Proposed climate change poses threats to both biodiversity and livelihood concerns.

3. A CHARACTERISATION OF ABIOTIC ENVIRONMENT AND VEGETATION TYPES SAMPLED ACROSS THE KAMIESBERG MOUNTAIN RANGE

Abstract: This chapter presents a characterisation of the vegetation types of the Kamiesberg. Each vegetation type sampled in the grazing analysis is characterised and the role of abiotic variables in determining vegetation boundaries is explored. Climate, in particular seasonal temperatures and rainfall, in combination with a distinct gradient of soil texture and chemistry, give rise to a heterogeneous landscape and in turn drive the diversity of the Kamiesberg. On this basis three broad ecoregions are suggested; a western, an upper, and an eastern ecoregion. The vegetation types followed in this study form a finer-scale community division, and are generally in keeping with those of previous authors. A further factor is that of habitat, where upland and lowland habitats are in some respects continuous across the range, and in others adopt the unique aspects of the vegetation types in which they are situated. Consideration of the six different vegetation types and emerging ecoregions in light of proposed environmental change suggests the predicted loss of numerous species is a real possibility. In making explicit the abiotic gradients determining change across the Kamiesberg, this study provides an important starting point for the formulation of future studies exploring the likely impacts of climate change in this conservation-worthy area.

3.1 INTRODUCTION

This chapter sets out to characterise the vegetation communities in which fence line contrast sites were located to test the central question to this thesis which is to examine grazing impacts. This characterisation involved an examination of vegetation communities and abiotic drivers. Mountains present interesting botanical research opportunities, where gradients in elements such as topography, altitude and climate drive changes in the vegetation which is consequently different to the surrounding plains (Schultze et al., 1996; Burke et al., 1998; Burke, 2001, 2002). The rapid expression of these changes allows us to explore the science of what drives community turnover on a relatively small scale (Beals, 1969). While this improves our understanding of localised dynamics it also enables us to address greater, less geographically-bound questions, relating to determinants of vegetation distribution and possible future change (Burke, 2001). It informs us of existing conditions and enables us to manage for future scenarios (Schmidt et al., 1994; Birch et al., 1999).

The Kamiesberg, situated in the conservation-worthy Succulent Karoo biome, exemplifies this type of research opportunity. The Succulent Karoo biome has some 5000 plant species, of which 40% are endemic to the biome, and is one of only two

globally-recognised biodiversity hotspots in an arid area (Hilton-Taylor, 1996; Mittermeier et al., 2004). Rising to some 1700 m over a relatively short distance, the Kamiesberg is host to a diversity of vegetation types (Adamson, 1938; Desmet and Helme, 2006; Mucina and Rutherford, 2006) and the consistent botanical work in the area over the last 150 years attests to its botanical importance. In his *Notes on the Vegetation of the Kamiesberg*, published in 1938, Adamson refers to several botanical surveys and studies undertaken in the region, including those by Drege over a hundred years earlier and Pearson in the early 1900s. In more recent years there has been work on specific floral elements (Rourke, 1990; Helme, 1992), the phytosociology (Eccles et al., 1999) and the ecology (Allsopp, 1999; Desmet and Cowling, 1999a; Joubert and Ryan, 1999; Seymour and Dean, 1999; Todd and Hoffman, 1999; Hoffman et al., 2003; Riginos and Hoffman, 2003; Petersen et al., 2004). Following on from this wealth of work the Kamiesberg itself, within this biome, has been acknowledged as an area of significant conservation worth (Lombard et al., 1999; Desmet and Helme, 2006).

Studies show the flora of the Kamiesberg as sensitive to land use with recorded compositional shifts in response to sustained heavy grazing by livestock (Todd and Hoffman, 1999) (also Chapter 4), and is predicted to be under threat from climate change (Broenniman et al., 2006; Midgley and Thuiller, 2007). A series of climate change models simulated for the Namaqualand area are in agreement in their predictions of directional change with increased summer rainfall and late summer wetting in the north east and decreased winter rainfall with substantial drying on the coastal plains (MacKellar et al., 2007). In the same analysis, an historical overview highlights the importance of topography in landscape level, and climatic heterogeneity (MacKellar et al., 2007).

Adamson (1938) noted that at the time of his work there had been no examination of the relationships among the different vegetation types. This still remains the case. The recognised conservation significance combined with predicted threats highlight a need to further our understanding of those factors influencing the vegetation of the Kamiesberg. Our current understanding is based on studies either focussed on localised areas within the Kamiesberg, or undertaken in the greater region. This paper aims to characterise the vegetation in which sampling in this study was carried out.

Selected sites, based primarily on the location of fence line sites to address the grazing question central to this thesis, also captured a number of distinct vegetation types. The selection of these vegetation types was subjective, based on an a priori understanding of the vegetation types of the area, largely formed through the work of Mucina and Rutherford (2006) with some refinement by the author. In characterising the vegetation at these sites across the Kamiesberg and exploring those abiotic factors influencing the distribution of the different vegetation types, this chapter hopes to further contribute to an understanding of the ecology of the area. An understanding of the geoclimatic and biogeographic drivers is an essential precursor to making management decisions (Schmidt et al., 1994; Broenniman et al., 2006). Once the underlying drivers are clarified the effects of land use and proposed climate change impacts can be explored.

3.2 METHODS

3.2.1 Site description

This study was conducted across the Kamiesberg, which is situated in Namaqualand in the Northern Cape Province of South Africa (Figure 3.1). The study area stretches approximately 50 km, from the inland regions adjacent to the coast in the west some 15 km from the sea, to the Buffels River basin in the east. To the north and south it is bounded by the towns of Kamieskroon and Garies respectively, with a breadth of roughly 20 km. The Kamiesberg is a large granite-gneiss intrusion surrounded predominantly, and relatively uniformly, by red and yellow weakly-structured apedal soils (Watkeys, 1999). Altitude ranges from 200 m above sea level in the western extreme, through to 1700 m at the highest sites, down to 1000 m in the east of the range, tapering to around 900 m on the Bushmanland plateau at the eastern extreme. The bulk of the study site falls within the winter rainfall region, where rainfall is low but relatively predictable (Desmet and Cowling, 1999b). To the extreme east with the transition into Bushmanland, some summer rainfall, in the form of thunderstorms, is experienced.

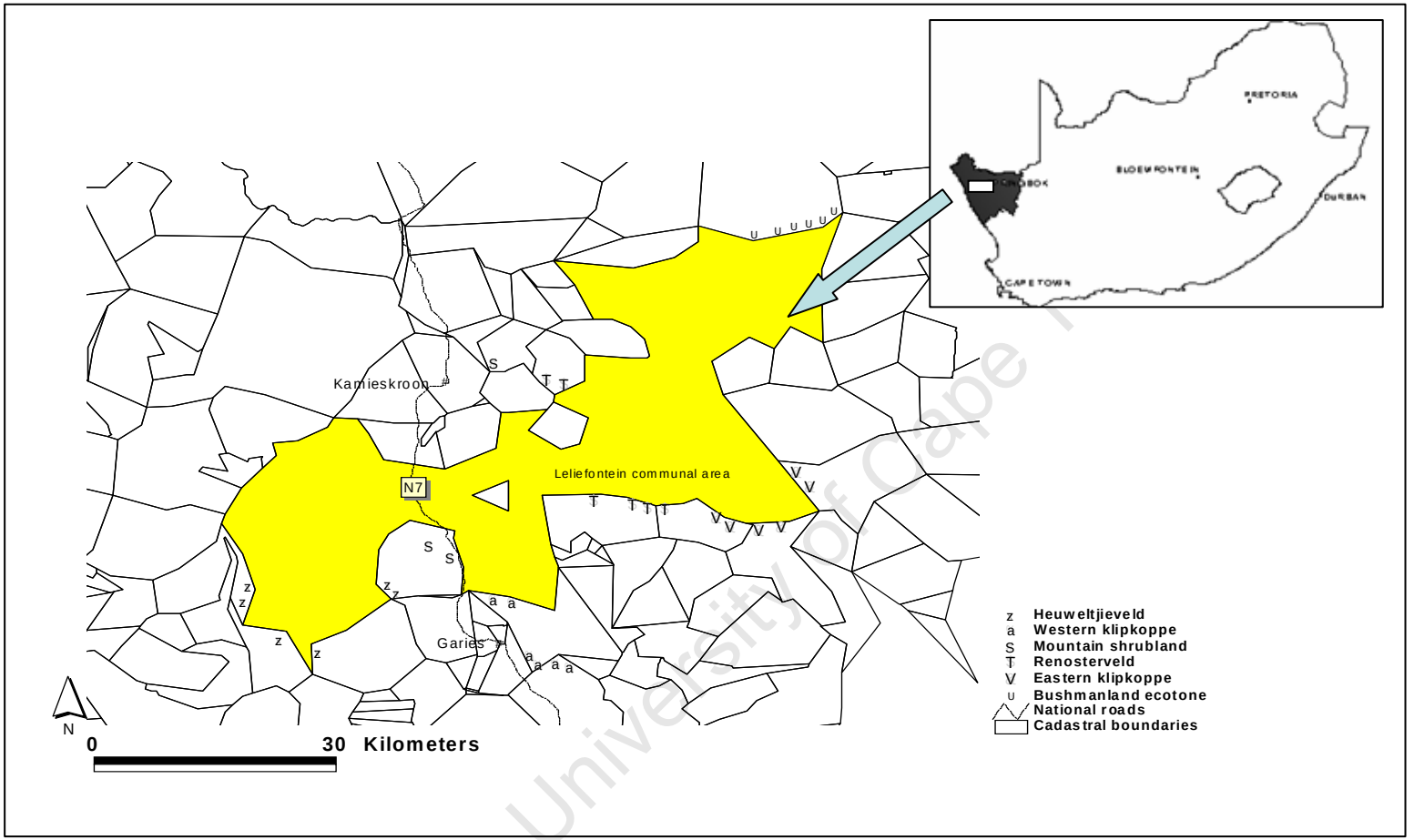


Figure 3.1 Map of the study site, indicating its position in relation to southern Africa. Also indicated are the sample sites according to vegetation types sampled. The Leliefontien communal area which straddles the Kamiesberg and around which this study is based, is the highlighted cadastral portion.

The vegetation of the region is broadly termed Succulent Karoo vegetation (Hilton-Taylor, 1996; Milton et al., 1997), and comprises more than sixty vegetation units or types (Mucina and Rutherford, 2006). Several authors have described and mapped the vegetation of the Kamiesberg and numerous descriptions of the distribution and types of vegetation in the area exist (Acocks, 1952; Low and Rebelo, 1996; Mucina and Rutherford, 2006). In this study a detailed examination of the *a priori* idenitified vegetation types (in which grazing related fence line sample sites were located) was undertaken along a pre-determined gradient to explore how and why species and associated vegetation types are distributed along a specific gradient of interest (Whittaker, 1956, 1978a, 1978b; Austin et al., 1984). The most apparent gradient in the case of the Kamiesberg is altitude, with an associated rainfall response. Since water is a critical driving factor in semi-arid systems (Noy-Meir, 1973; Abd el-Ghani and Amer, 2003) sampling was carried out primarily across this gradient. Sites were selected based on the overarching question of this thesis which is an examination of grazing impacts across a range of vegetation types in the Kamiesberg. These sites were placed in a number of different vegetation types, capturing much of the community diversity of the mountain range, and informed by an existing understanding of the vegetation, based on previous mapping efforts and the researcher's prior knowledge of the vegetation of the area. Sampling was infomed by both pre-determined macro-scale vegetation units in the area and a finerscale habitat consideration. The Kamiesberg is characterised by a mosaic of rocky upland and sandy lowland habitats, and this habitat variability was also included in the sampling strategy (Adamson, 1938). The respective ratio of lowland to upland area varies across the mountain range with a greater proportion of upland areas at the higher altitudes. The vegetation types sampled in this study were termed (moving from west to east) Heuweltjieveld, Western klipkoppe, Mountain shrubland, Renosterveld, Eastern klipkoppe and Bushmanland ecotone vegetation. These are based most closely on the recent work of Mucina and Rutherford (2006) with some refinement on the part of the author. Synonyms for the vegetation types used in this and previous studies are shown in Table 3.1. A representative photograph of each vegetation type, including (where appropriate) upland and lowland habitats, is given in Figure 3.2.

Table 3.1 Vegetation type terminology used in this study with synonyms from previous authors.

This study	Adamson (1938)	Acocks (1953)	Low and Rebelo (1996)	Mucina and Rutherford (2006)
Heuweltjieveld lowland	No equivalent	Succulent Karoo	Lowland succulent Karoo	Namaqualand Heuweltjieveld
Heuweltjieveld upland	No equivalent	Succulent Karoo	Lowland succulent Karoo	Namaqualand Heuweltjieveld
Western klipkoppe lowland	Karoo communities	Succulent Karoo	Lowland succulent Karoo	Namaqualand Blomveld
Western klipkoppe upland	Karoo communities	Namaqualand Broken Veld	Upland Succulent Karoo	Namaqualand Klipkoppe Shrubland
Mountain shrubland	West facing escarpment slope community	Namaqualand Broken Veld	Upland Succulent Karoo	Kamiesberg Mountains Shrubland
Renosterveld lowland	Rhenosterveld	Mountain Renosterbosveld	North-western Mountain Renosterveld	Namaqualand Granite Renosterveld
Renosterveld upland	Communities marginal to Rhenosterveld	Mountain Renosterbosveld	North-western Mountain Renosterveld	Namaqualand Klipkoppe Shrubland
Eastern klipkoppe lowland	Karoo communities	Namaqualand Broken Veld	Upland Succulent Karoo	Namaqualand Blomveld
Eastern klipkoppe upland	Communities marginal to Rhenosterveld	Namaqualand Broken Veld	Upland Succulent Karoo	Namaqualand Klipkoppe Shrubland
Bushmanland ecotone lowland	No equivalent	Namaqualand Broken Veld / False Succulent Karoo	Upland Succulent Karoo / Bushmanland ecotone	Bushmanland arid grassland / Platbakkies succulent shrubland ecotone
Bushmanland ecotone upland	Karoo communities	Namaqualand Broken Veld / False Succulent Karoo	Upland Succulent Karoo / Bushmanland ecotone	Bushmanland arid grassland / Platbakkies succulent shrubland ecotone

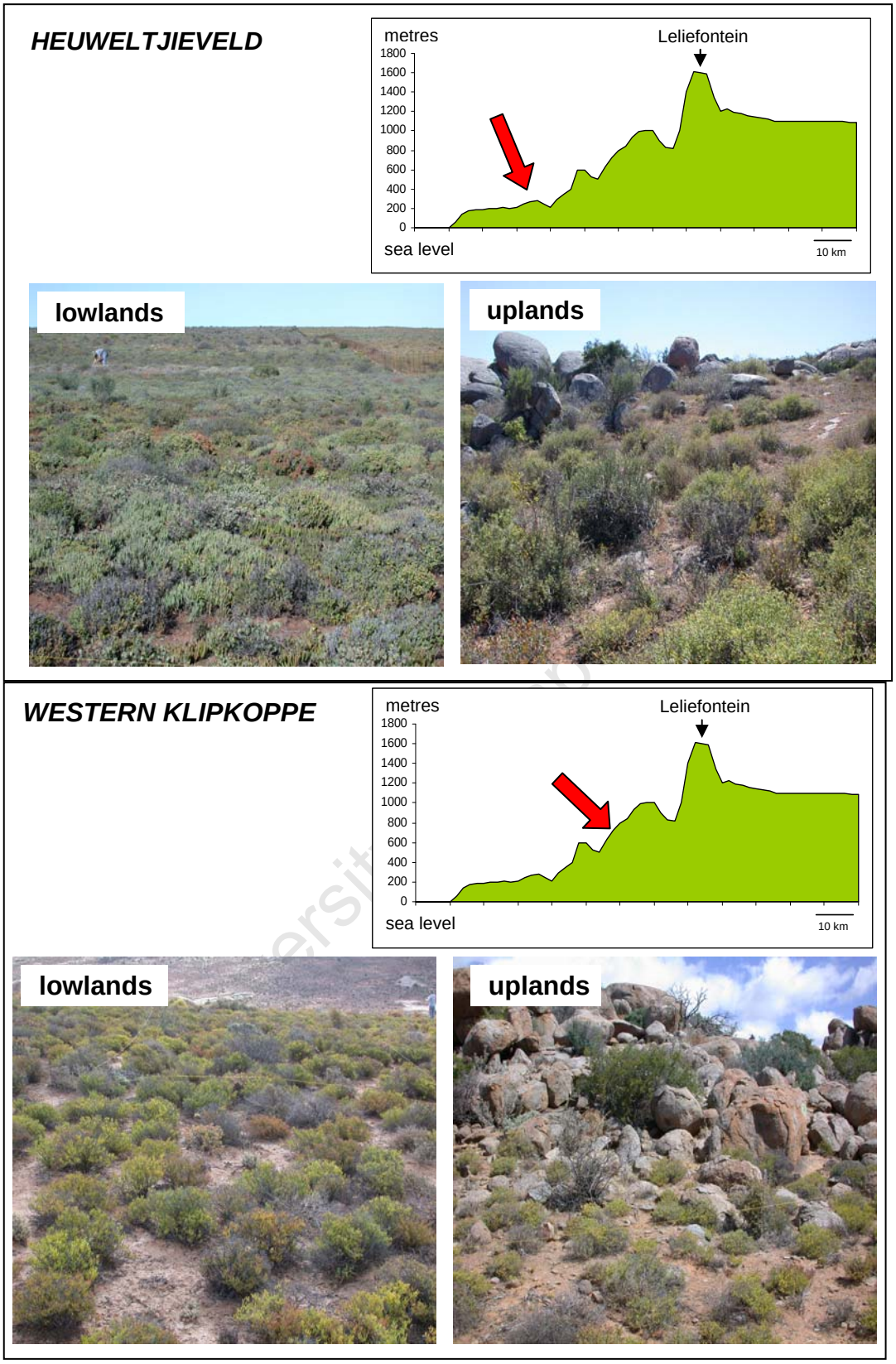


Figure 3.2 a. Representative photographs of lowland and upland habitats in the Heuweltjieveld and Western klipkoppe vegetation types. An arrow indicates where each vegetation type lies along the altitudinal profile of the Kamiesberg presented in the top right hand corner of each picture.

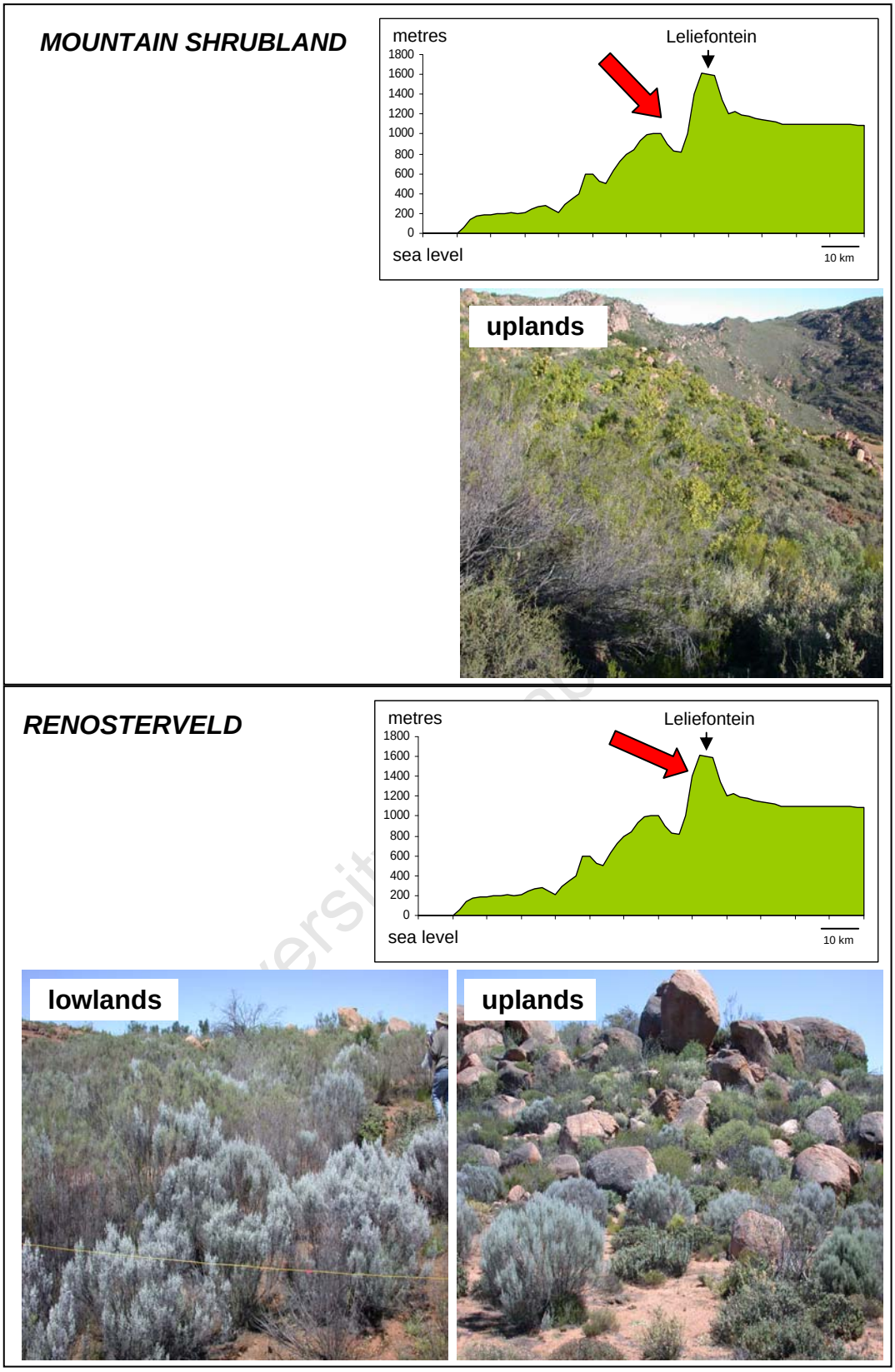


Figure 3.2 b. Representative photographs of the upland habitat in the Mountain shrubland and lowland and upland habitats in the Renosterveld vegetation types. An arrow indicates where each vegetation type lies along the altitudinal profile of the Kamiesberg presented in the top right hand corner of each picture.

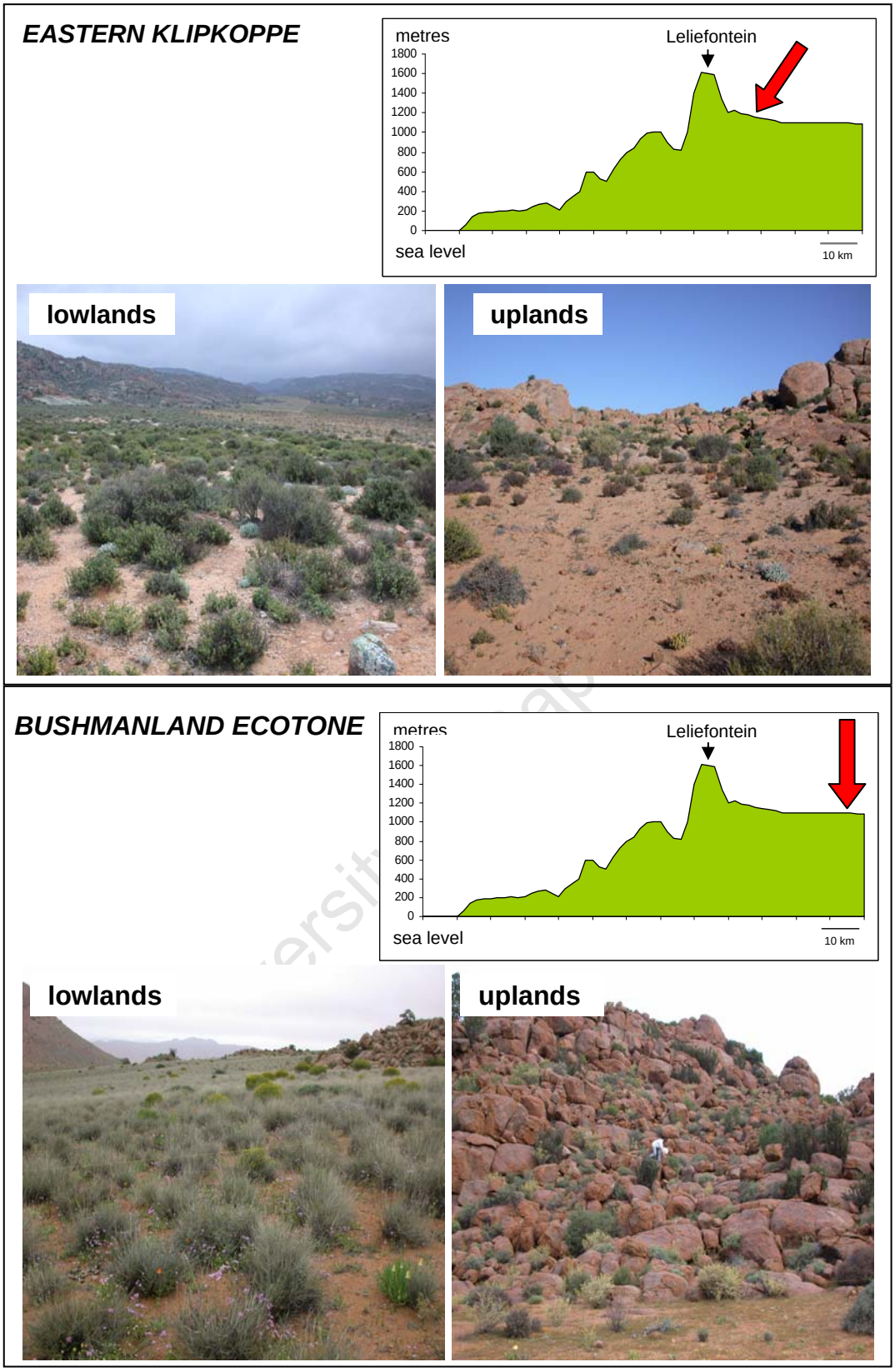


Figure 3.2 c. Representative photographs of lowland and upland habitats in the Eastern klipkoppe and Bushmanland ecotone vegetation types. An arrow indicates where each vegetation type lies along the altitudinal profile of the Kamiesberg presented in the top right hand corner of each picture.

3.2.2 Data collection

Thirty-three modified Whittaker plots (Stohlgren et al., 1997; Stohlgren et al., 1998) were used to sample the vegetation across the study area, with six plots in the Heuweltjieveld, Western klipkoppe, Renosterveld, Eastern klipkoppe and Bushmanland ecotone vegetation types and three plots in the Mountain shrubland vegetation. These plots were spread evenly between upland and lowland habitats (i.e. three in each habitat). The Mountain shrubland vegetation type is restricted to slopes, and in this vegetation type no lowland component exists. Sites were selected so as to minimise variability in slope and aspect, as well as for accessibility. A minimum avoidance distance of 50 m was given to known stock posts and water points to avoid the 'sacrifice zone' established for the area (Riginos and Hoffman, 2003). Old lands (previously cropped areas) were also avoided. Some remnant Fynbos patches exist on the highest peaks of the Kamiesberg (Mucina and Rutherford, 2006). These were not included in this study as they did not fit with the remit of the greater research project that this chapter forms a part of. These remnant patches have however received considerable attention recently for their conservation value (Desmet and Helme, 2006).

Sampling was carried out in the spring of 2002. To minimise the effects of heavy grazing on plant species composition and cover, vegetation sampling was only carried out only on less heavily-grazed, privately owned farms (Todd and Hoffman, 2000). The sampling technique followed was according to the multi-scale modified Whittaker plot (Stohlgren et al., 1997; Stohlgren et al., 1998). The modified Whittaker plot comprises a series of nested subplots, with ten 1 m^2, two 10 m^2, and one 100 m^2 subplots all nested in a 1000 m^2 plot. In each of the ten 1 m^2 subplots species composition and a visual estimate of percentage cover was recorded, and in each subsequent subplot, cumulative species were recorded. Taxonomic nomenclature follows Germishuizen and Meyer (Germishuizen and Meyer, 2003). Species were assigned to one of the following life history and growth form categories: annual herbs, annual grasses, geophytes, perennial grasses, dwarf shrubs (including all perennials of less than 25 cm in height, and all perennial herbs), woody shrubs (including all woody shrubs of more than 25 cm in height), succulents (including both stem and leaf succulents), and trees.

Also recorded at each site were slope, aspect, a visual estimate of percentage rock cover, percentage rockiness of the soil itself, and soil depth. Slope was measured with an Abney level, and soil depth was measured in open areas by hammering a metal stake (1 cm diameter) into the soil until bedrock was reached. Five depth measurements were taken at each site and the mean value calculated. A composite soil sample was taken at each site from three soil samples taken to a depth of 10 cm from open areas for textural and chemical analysis. Median annual precipitation, frost days, and maximum January and July temperatures were obtained from the South African Atlas of Agrohydrology and Climatology (Schultze, 1997). This atlas gives modelled layers for which site point measures were taken, which allows for a single measure for every site, unlike station data, allowing for the calculation of a coefficient of variation in each case. For these abiotic data an additional set of 33 samples were included taken from communal sites, following analysis that showed land management did not significantly alter these abiotic variables.

3.2.3 Data processing and statistical analyses

Soil samples were analysed for the following chemical properties: pH; resistance; total carbon; total nitrogen; potassium; phosphorus and exchangeable cations (Mg, Ca, K and NA). pH was determined in 1M KCl (McClean, 1982). Total carbon was determined using the Walkley-Black method and total nitrogen was determined by digestion in a LECO FP-528 nitrogen analyser (Nelson and Sommers, 1982). Exchangeable cations were determined in a 1M ammonium acetate extract (Doll and Lucas, 1973). Cation exchange capacity (CEC) was determined at pH 7 by saturation with 0.2 M ammonium acetate. Ammonium was displaced with K2SO4 and determined by Kjeldahl distillation (Peech, 1965). Soil texture was analysed using the Bouyoucos particle size method (Bouyoucos, 1962).

Vegetation types were assigned a fire category ranging from 1 (will not burn), through 2 (may rarely burn), to 3 (fire-prone). This was on the basis of our understanding that Renoserveld is fire-prone (Bond, 1997) and that the highly woody Mountain shrubland, immediately adjacent to the Renosterveld is described as occasionally

burning by local farmers (Schreuder, pers. comm.)[2], while karroid shrublands are described as a fire-free vegetation (Bond, 1997).

Single-factor ANOVAs and Tukey's Honest Significant Differences post-hoc analysis were used to explore significant differences in growth forms across vegetation types (totals for lowland and upland habitats grouped within vegetation types), and for the lowland and upland habitats independently. When data were non-parametric the Kruskal-Wallis analysis of variance (ANOVA) for non-parametric data and the post-hoc multiple comparisons of means were used. To determine factors driving turnover along the gradient, altitude and climatic variables were grouped across habitat types within vegetation types and statistically analysed with the Kruskal-Wallis ANOVA for non-parametric data, and post-hoc relationships were determined with the multiple comparisons of means test. Remaining topographical, and physical and chemical soil variables were also analysed using the Kruskal-Wallis ANOVA for non-parametric data for each vegetation type (totals for lowland and upland habitats grouped within vegetation types) and lowland and upland habitats independently. The topographical and soil data were also analysed with a Nested-ANOVA, where habitat considerations are nested within each vegetation type, which is the major factor of interest; to examine to what degree these abiotic elements are a function of vegetation type or habitat (Quinn and Keough, 2002). In some instances variables were transformed to attain normality. In exploring consistent abiotic variation associated with habitat types across the entire mountain range, upland and lowland habitats were grouped and analysed for statistical differences with a Mann-Whitney U test.

3.3 RESULTS

3.3.1 Vegetation descriptors

The ten most frequently encountered species in each vegetation type as well as the ten most dominant, in terms of percentage cover, are presented in Table 3.1. Plant cover generally follows a humped curve, where cover is highest at the higher altitudes, with

[2] Mr Gawie Schreuder owns the farm Naartjiesdam in the Kamiesberg.

the exception of the Heuweltjieveld lowlands where cover is equivalent to the Renosterveld lowlands (Figure 3.3a). Cover on the lowland areas is generally higher than the upland equivalent. However, this is frequently a function of rock cover and available soil. The lowest total plant cover is found on the Bushmanland ecotone uplands which are extremely rocky (Figure 3.4 b and Table 3.4b). In contrast species number is generally greatest on the uplands (Figure 3.4c), and the Simpson's diversity index, accounting for abundance patterns and species richness (Began et al., 1986), shows the uplands to be consistently more diverse than the lowlands, with the exception of Renosterveld which has a diversity index of 8.1. Mountain shrubland has the highest diversity index at 8.8, with the Western klipkoppe uplands and Bushmanland ecotone uplands both with 8.6. The lowest diversity index is for the Bushmanland ecotone lowlands, with an index of 5.5. Mean plant height is significantly higher on the uplands and broadly tracks the altitudinal gradient, despite some structurally lower vegetation in the Eastern klipkoppe and structurally higher vegetation in the Bushmanland ecotone (Figure 3.4d).

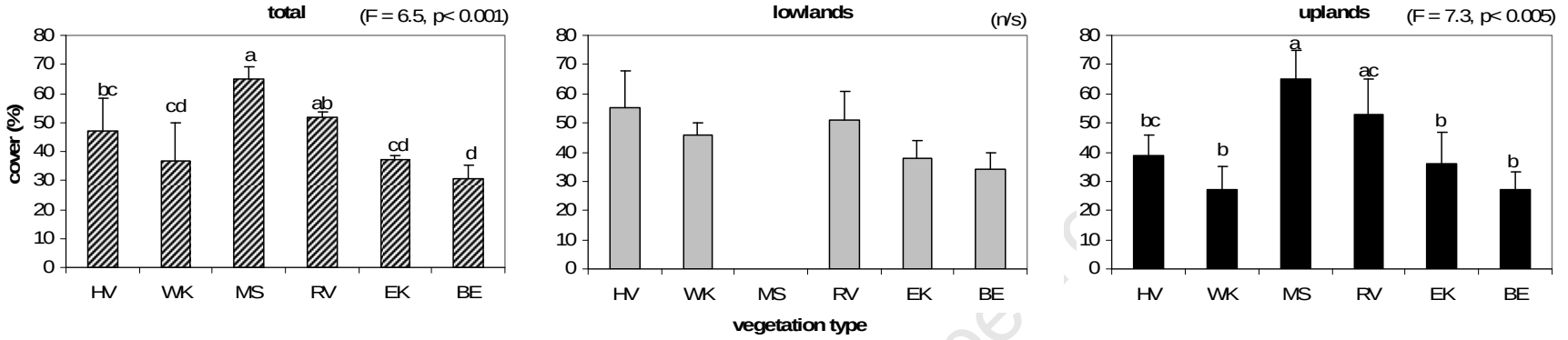
Table 3.2 Ten most common (+) and ten most dominant (/) species recorded for each vegetation and habitat type.

	Heuweltjieveld		Western klipkoppe		Mountain shrubland	Renosterveld		Eastern klipkoppe		Bushmanland ecotone	
	lowland	upland	lowland	upland	upland	lowland	upland	lowland	upland	lowland	upland
Galenia sarcophylla	+/	+	+/	+/							
Drosanthemum oculatum	+/	+/		+							
Rhynchopsidium pumilum	+	+	+/							+/	+
Didelta carnosa	+		+	+							
Bromus pectinatus	+										
Tetragonia fruticosa	+	+/	+								
Salsola sp.	+/										
Aridaria vespertina	+										
Ruschia fugitans	+/								/		
Zygophyllum cordifolium	+/	/									
Felecia merxmuelleri	/	+				+				+	
Cephalophyllum ebracteatum	/										
Leipoldtia laxa	/			+/							
Drosanthemum schoenlandianun	/										
Ruschia viridifolia	/			/							
Euphorbia mauritanica		/								/	
Antimima tuberculosa		/									
Arctotis argentec			/								
Ruschia aggregata			/								
Ruschia macownii			/								
Berkheya spinossisima		+	/								
Rhus undulata		+/		+	+/				/		+/
Manochlamys albicans		+/									
Zygophyllum morgsana	/	+/	+/	/							
Ballota africana		+									
Hypertelis salsoloide			+								
Trachyandra revoluta			+								
Tetragonia glauca			+/	/							
Atriplex lindleyi			+	+							
Aridaria serotinc		/	+/								
Lycium ferocissimum				+				/			/
Hirpicium alienatum				+				+/	+/		
Lebeckia multiflora		/		+/	+/				/		
Ehrharta brevifolia				/							
Antimima compressa				/							
Codon royenii				/							
Ruschia goodiae				/							
Didelta spinosa				+	+/						
Schmidtia kalahariensis					+						

	Heuweltjieveld		Western klipkoppe		Mountain shrubland	Renosterveld		Eastern klipkoppe		Bushmanland ecotone	
	lowland	upland	lowland	upland	upland	lowland	upland	lowland	upland	lowland	upland
Ehrharta barbinodis					+			+	+		
Montinia caryophyllaceae					+						
Euryops laterifolius					+/		+				
Asparagus capensis					+		+				
Oederoa genistifolia					+/	+					
Dodonaea viscosa					+/						
Struthiola leptantha					/						
Pteronia incana					/		/				
Lebeckia cytisoides					/						
Chrysochoma ciliata						+	+		+		
Elytropappus rhinocerotus					/	+/	+/				
Senecio cinerascens						+	+/				
Clutia thunbergii						+/					
Helichrysum leontonyx						+					
Sutherlandia frutescens						+					
Moraea fugax						+					
Ehrharta calycina						+					
Diospyros glabra						/					
Dimorphotheca cuneata						/					
Gazania tenuifolia						/					
Ficinia nigrescens						/					
Stachys rugosa						/					
Ruschia elineata						/	/				
Restio cymosus							+/				
Senecio juniperinus							+				
Felicia filifolia						/	+				
Coleonema juniperinum							+/				
Merxmuellera dura							+/				
Cliffortia ruscifolia							/				
Eriocephalus africanus							/				
Phylica montana							/				
Leysera tenella								+			
Gazania heterochaeta								+			
Moraea tortilis								+			
Cheiridopsis namaquensis								+			
Eriocephalus ericoides								+/	+/		+
Euphorbia decussata								+/	+/	/	
Ruschia robusta								+/	/		
Cheiridopsis denticulata								+/			
Drosanthemum hispidum								/			
Galenia africana								/			
Leipoldtia schultzei								/			

	Heuweltjieveld		Western klipkoppe		Mountain shrubland	Renosterveld		Eastern klipkoppe		Bushmanland ecotone	
	lowland	upland	lowland	upland	upland	lowland	upland	lowland	upland	lowland	upland
Polymita abliflora									+/		
Pelargonium dasyphyllum									+		
Tripteris sinuata									+		
Antizoma miersiana									+		/
Pentzia incana								/	+		+/
Othonna abrotanifolia									/		
Stipagrostis brevifolia										+/	/
Conicosia elongata										+/	
Grielum humifusum										+/	
Gorteria personata										+/	
Lasiospermum brachyglossum										+	
Zygophyllum retrofractum									/	+	
Heliophila variabilis										+	+
Aptosimum spinescens										+	
Tetragonia sarcophylla										/	
Hermannia trifurca										/	
Senecio arenarius										/	+
Senecio elegans										/	
Hermannia amoena											+/
Dyerophytum africanum											+
Cissampelos capensis											+
Enneapogon scaber											+
Acanthopsis spathularis											/
Blepharis furcata											/
Cadaba aphylla											/
Pteronia divaricata											/

a) plant cover



b) plant cover as a function of available area

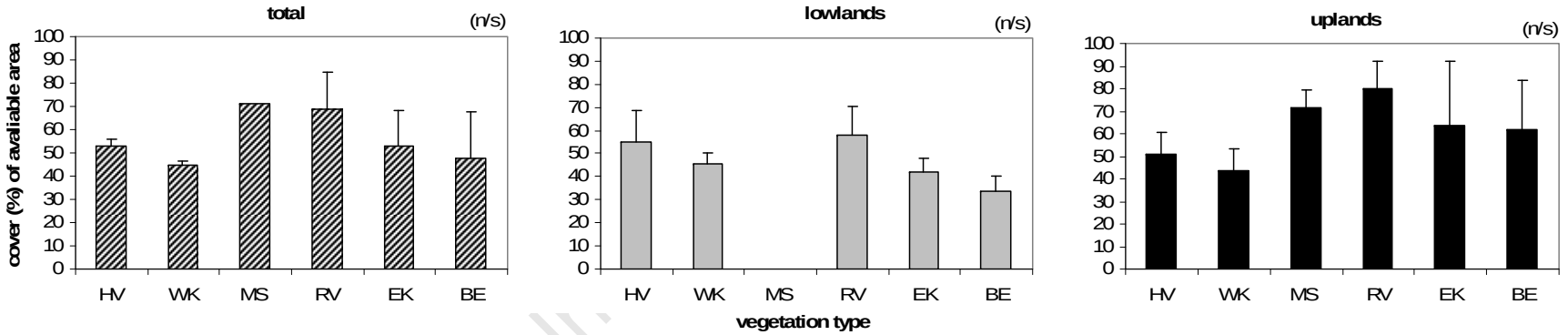
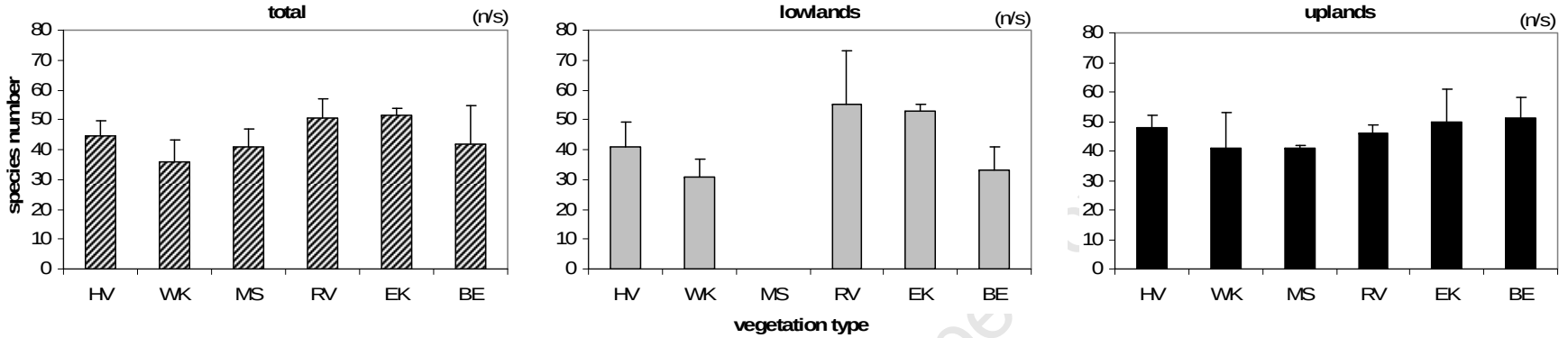


Figure 3.3 a and b Mean percentage (±SD) for (a) total plant cover and (b) cover as a function of available area (less rock cover) for each vegetation type (total) and lowland and upland habitat types. Each y-axis presents a west-east gradient where HV is Heuweltjieveld, WK is Western klipkoppe, MS is Mountain shrubland, RV is Renosterveld, EK is Eastern klipkoppe, and BE is Bushmanland ecotone. Statistical results are given at the top right hand corner of each graph (n = 12 for totals, except for MS where n = 6 for totals, n = 6 for each habitat type). As Mountain shrubland has no lowland habitat no value is given on the lowlands graphs, its position on the graph is maintained for consistency.

c) species number



d) plant height

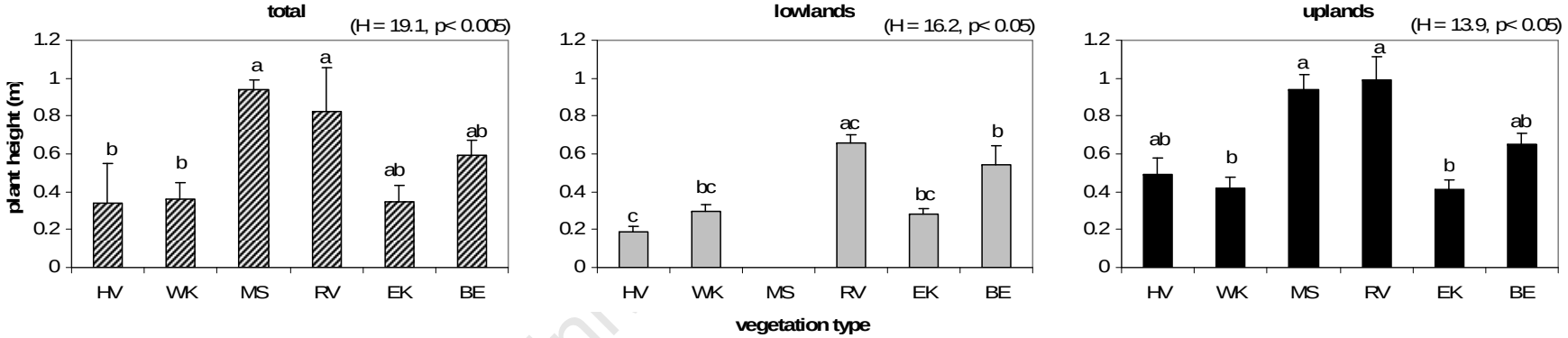
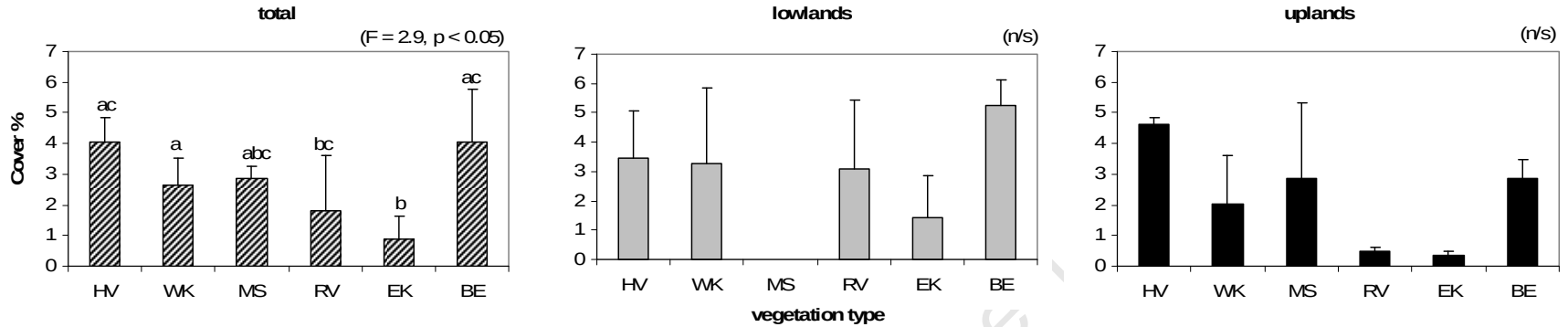


Figure 3.3 c and d Mean number (c) and height (d) (±SD) for (c) species number and (d) plant height for each vegetation type (total) and lowland and upland habitat types. Each y-axis presents a west-east gradient where HV is Heuweltjieveld, WK is Western klipkoppe, MS is Mountain shrubland, RV is Renosterveld, EK is Eastern klipkoppe, and BE is Bushmanland ecotone. Statistical results are given at the top right hand corner of each graph (n = 12 for totals, except for MS where n = 6 for totals, n = 6 for each habitat type). As Mountain shrubland has no lowland habitat no value is given on the lowlands graphs, its position on the graph is maintained for consistency.

Annual cover is almost consistently higher on the lowland sites and annual grass cover is largely confined to the western vegetation types and is more dominant on the rocky uplands (Figure 3.4 a- h). Geophyte cover is patchy and varied across all vegetation types with the exception of relatively large contributions in the Heuweltjieveld uplands and Mountain shrubland vegetation types. Variance for all annual growth forms is high between plots. Perennial grass cover is largely restricted to the Bushmanland ecotone and the Renosterveld vegetation types. Woody shrubs show the same humped relationship as total plant cover, dominating the higher altitude sites. The reverse is true of succulent cover which is negligible in the Renosterveld and Mountain shrubland vegetation types, but dominates the lowlands of the Heuweltjieveld, Western klipkoppe and Eastern klipkoppe vegetation types. Trees are largely restricted to Mountain shrubland, with some in the upland habitats of other vegetation types, in particular the Bushmanland ecotone uplands.

a) annuals



b) annual grass

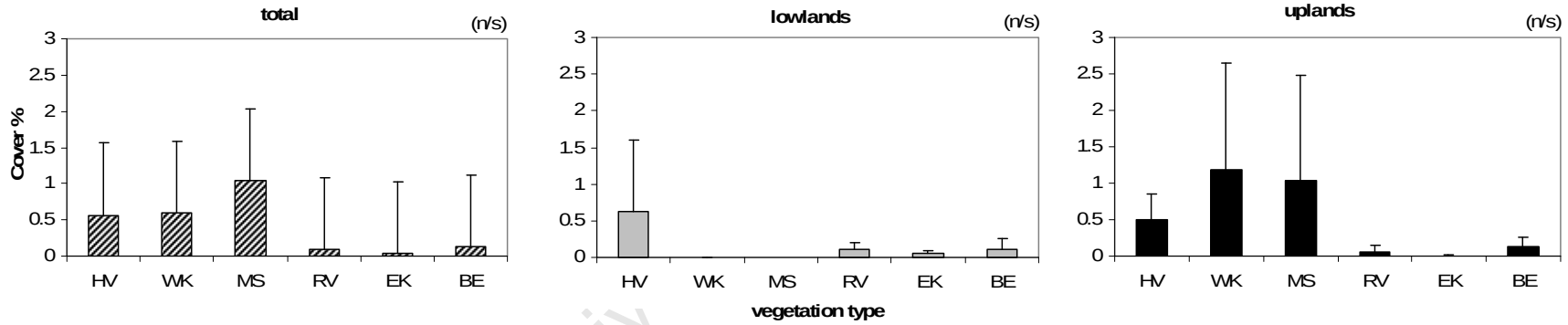
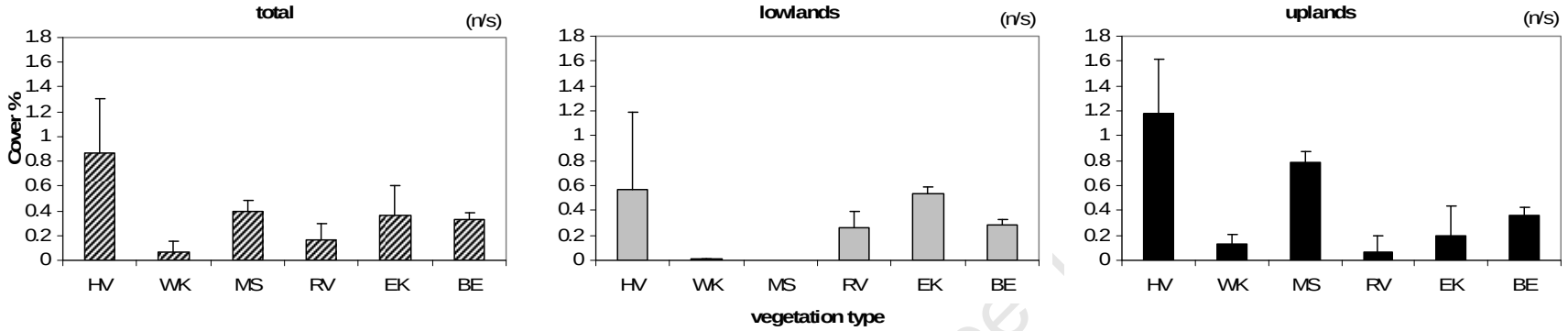


Figure 3.4 a and b Mean percentage cover (±SD) for growth forms (a) annuals and (a) annual grass for each vegetation type (total) and lowland and upland habitat types. Each y-axis presents a west-east gradient where HV is Heuweltjieveld, WK is Western klipkoppe, MS is Mountain shrubland, RV is Renosterveld, EK is Eastern klipkoppe, and BE is Bushmanland ecotone. Statistical results are given at the top right hand corner of each graph (n = 12 for totals, except for MS where n = 6 for totals, n = 6 for each habitat type). As Mountain shrubland has no lowland habitat no value is given on the lowlands graphs, its position on the graph is maintained for consistency.

c) geophytes



d) perennial grass

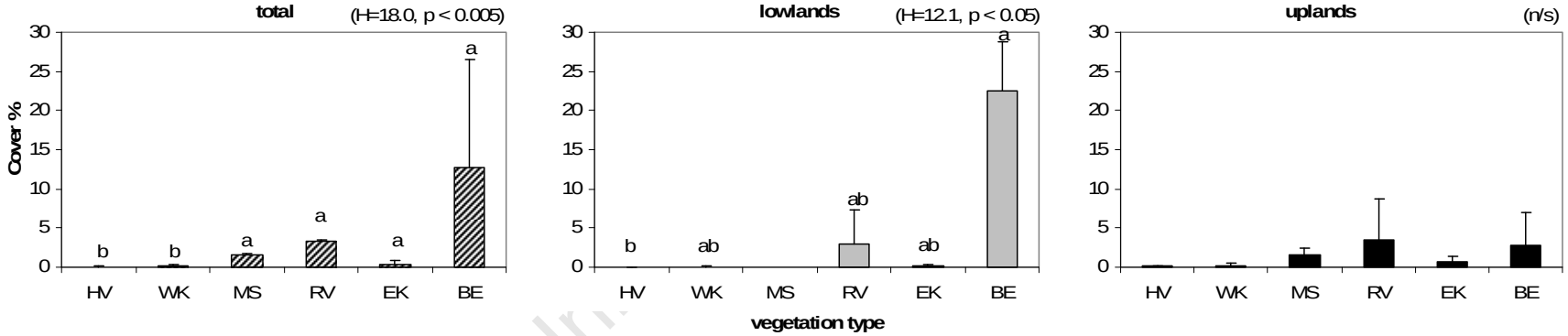
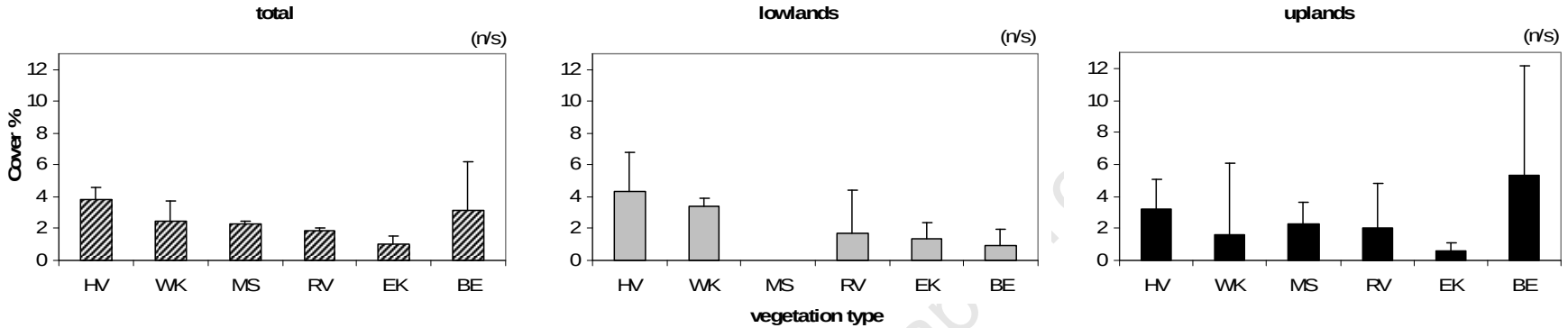


Figure 3.4 c and d Mean percentage cover (±SD) for growth forms (c) geophytes and (d) perennial grass for each vegetation type (total) and lowland and upland habitat types. Each y-axis presents a west-east gradient where HV is Heuweltjieveld, WK is Western klipkoppe, MS is Mountain shrubland, RV is Renosterveld, EK is Eastern klipkoppe, and BE is Bushmanland ecotone. Statistical results are given at the top right hand corner of each graph (n = 12 for totals, except for MS where n = 6 for totals, n = 6 for each habitat type). As Mountain shrubland has no lowland habitat no value is given on the lowlands graphs, its position on the graph is maintained for consistency.

e) dwarf shrubs



f) woody shrubs

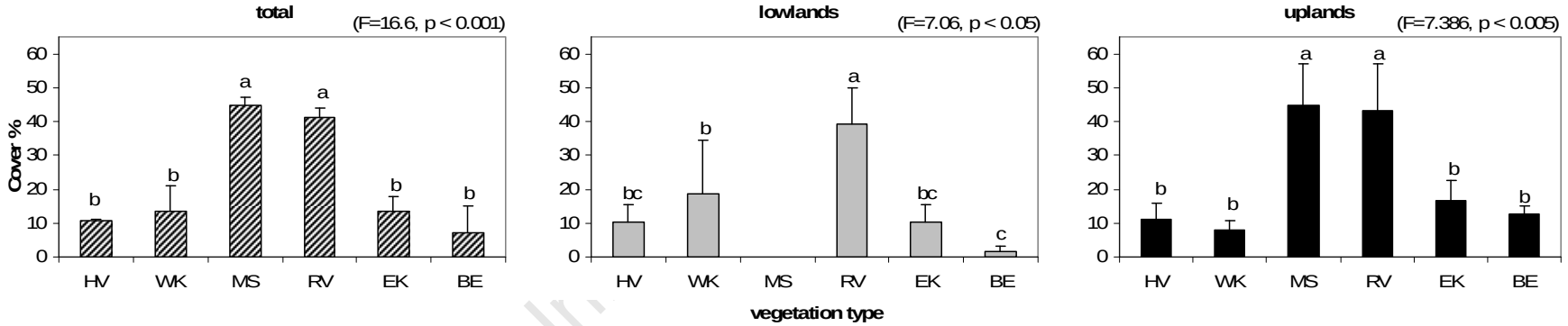
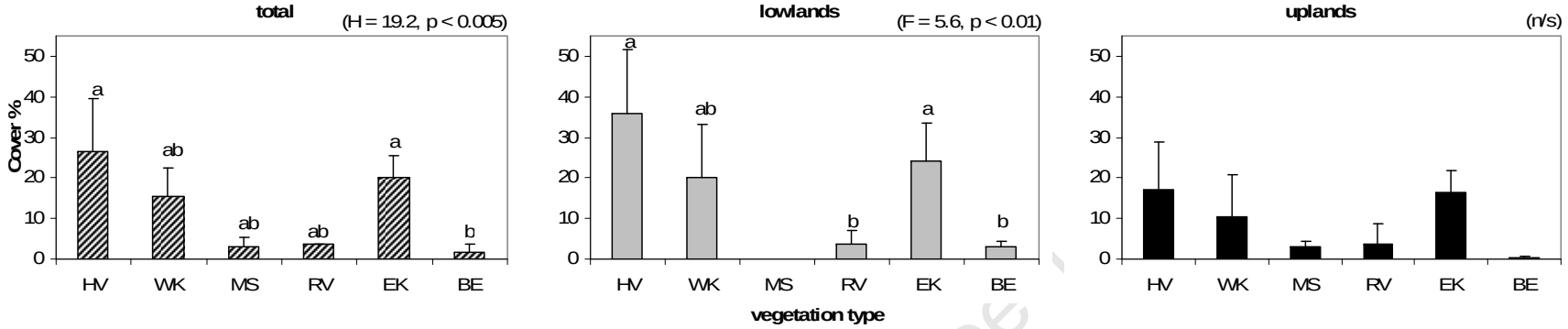


Figure 3.4 e and f Mean percentage cover (±SD) for growth forms (e) dwarf shrubs and (f) woody shrubs for each vegetation type (total) and lowland and upland habitat types. Each y-axis presents a west-east gradient where HV is Heuweltjieveld, WK is Western klipkoppe, MS is Mountain shrubland, RV is Renosterveld, EK is Eastern klipkoppe, and BE is Bushmanland ecotone. Statistical results are given at the top right hand corner of each graph (n = 12 for totals, except for MS where n = 6 for totals, n = 6 for each habitat type). As Mountain shrubland has no lowland habitat no value is given on the lowlands graphs, its position on the graph is maintained for consistency.

g) succulents



h) trees

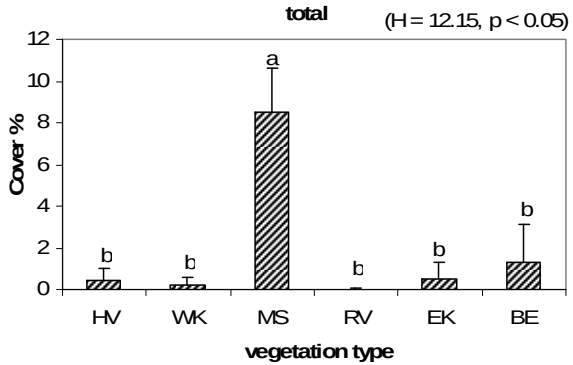


Figure 3.4 g and h Mean percentage cover (±SD) for growth forms (g) succulents and (h) trees for each vegetation type (total) and lowland and upland habitat types. Each y-axis presents a west-east gradient where HV is Heuweltjieveld, WK is Western klipkoppe, MS is Mountain shrubland, RV is Renosterveld, EK is Eastern klipkoppe, and BE is Bushmanland ecotone. Statistical results are given at the top right hand corner of each graph (n = 12 for totals, except for MS where n = 6 for totals, n = 6 for each habitat type). As Mountain shrubland has no lowland habitat no value is given on the lowlands graphs, its position on the graph is maintained for consistency. As no trees were recorded on the lowlands only the total figures (which are equivalent to upland figures) are shown here.

3.3.2 Abiotic variables

Altitude, and climate which closely tracks the altitudinal gradient, are significant environmental drivers differentiating between vegetation types across the range, and broadly denoting a western, upper and eastern region across the gradient (Table 3.3). The coefficient of variation of rainfall is highest at the western and eastern extremes. The Heuweltjieveld and Western klipkoppe share a fairly uniform climatic regime. Mountain shrubland groups variably with either the lower, more western portions, for example in terms of frost days and some seasonal temperature variables and then with the higher altitude, or upper regions dominated by the Renosterveld, with respect to rainfall and variation in rainfall. With respect to climate, the Eastern klipkoppe forms part of this upper region, sharing a similar climatic envelope with the Renosterveld, with slightly less rainfall and less reliable rainfall. The Bushmanland ecotone has some similar seasonal temperatures as this more western, upper region, but is considerably more arid, experiences far less frost and has a higher coefficient of variation in rainfall.

Table 3.3 The mean (±SD) plot values of the abiotic variables listed in lowland and upland vegetation types in the Kamiesberg. The Kruskal-Wallis H-statistic is given, for which all values are significant at the $p < 0.001$ level ($n = 66$). Post-hoc results based on z-scores from a multiple comparison of mean ranks are indicated by superscripts.

	Heuweltjieveld	Western klipkoppe	Mountain shrubland	Renosterveld	Eastern klipkoppe	Bushmanland ecotone	H-statistic
Altitude (masl)	246 ±65^{a}	365 ±100^{ac}	797 ±114^{ab}	1249 ±137^{b}	1077 ±45^{b}	892 ±23^{bc}	59.3
Rainfall (mm)	136.2 ±27.3^{a}	175.7 ±22.8^{ac}	258.6 ±35.5^{bc}	266.0 ±40.0^{b}	182.5 ±8.1b^{cd}	129.6 ±17.8^{ad}	54.7
CV rainfall (%)	38.7 ±0.5^{ac}	37.9 ±1.0^{ad}	35.8 ±1.0^{bc}	35.6 ±0.8^{b}	38.0 ±0.0^{a}	39.1 ±0.3^{bcd}	50.8
Mean Maximum Temperature January (ºC)	28.8 ±0.4^{ac}	29.9 ±0.3^{a}	26.8 ±0.4^{bc}	25.3 ±0.5^{b}	28.0 ±0.0^{bc}	30.0 ±0.0^{a}	62.8
Mean Maximum Temperature July (ºC)	18.6 ±0.5^{a}	18.8 ±0.3^{a}	16.5 ±0.8	13.6 ±1.0^{b}	15.3 ±0.5^{bc}	16.9 ±0.3^{ac}	60.4
Mean Minimum Temperature January (ºC)	14.2 ±0.4^{a}	13.9 ±0.2^{ac}	12.7 ±0.5^{bc}	12.1 ±0.4^{b}	12.0 ±0.0^{b}	13.0 ±0.0^{ab}	59.8
Mean Minimum Temperature July (ºC)	6.8 ±0.4^{a}	5.9 ±0.2^{a}	4.5 ±0.8^{ab}	2.3 ±0.5^{b}	3.0 ±0.0^{b}	3.2 ±0.4^{b}	59.9
Mean no. frost days	1.2 ±0.4^{a}	1.9 ±0.4^{ac}	8.1 ±7.3^{ab}	32.2 ±4.1^{b}	33.0 ±5.2^{b}	16.5 ±4.6^{bc}	58.6
Fire index	3	3	2	1	3	3	-

Soil texture (Tables 3.4 a, b and c) and chemistry (Tables 3.5 a, b and c) reinforce the broad divisions of the gradient into western, upper and eastern components. The soils to the west of the Kamiesberg have a greater proportion of fine sand and limited stone content, while those of the Bushmanland ecotone in the east are significantly coarser, with a higher stone content. Mountain shrubland, Renosterveld and Eastern klipkoppe soils are consistently more acidic than those to the west and the east. Soil resistance is considerably lower in the Heuweltjieveld and Western klipkoppe soils to the west of the range, a pattern which is largely echoed for soil sodium content. Soil exchangeable calcium is low in the Eastern klipkoppe and Mountain shrubland soils, in contrast to the higher values to the west. Exchangeable magnesium content is higher among the soils to the west, and lower at the eastern extreme, with significant differences between the Heuweltjieveld and Bushmanland ecotone soils. Percentage soil nitrogen is highest at the top of the Kamiesberg in the Renosterveld. Low soil nitrogen to the east of the Kamiesberg serves to differentiate this region from other sites in the study area. Percentage soil carbon is higher on the western and upper components of the gradient, with a patch of higher soil carbon among the Bushmanland ecotone uplands. The nested-ANOVA (included in Tables 3.4 a and 3.5 a) showed differences in slope, percentage rock cover, and soil phosphorus content to be a function of habitat type as situated in its associated vegetation type, whereas soil magnesium is a function of vegetation type irrespective of habitat. Other significant differences in this analysis were by both vegetation type and habitat.

Table 3.4a Means (±SD) of physical soil properties for combined upland and lowland habitat types in each vegetation type in a west-east gradient across the Kamiesberg. Significance levels are shown as: * = p < 0.05; ** = p < 0.005; *** = p < 0.001 (n = 12, except for Mountain shrubland where n = 6). Post-hoc variation between vegetation types is indicated in superscript above each variable. Results of the nested-ANOVA are presented in the last two columns.

	Heuweltjieveld	Western klipkoppe	Mountain shrubland	Renosterveld	Eastern klipkoppe	Bushmanland ecotone	H-statistic and significance level	Vegetation f-statistic	Vegetation x (habitat type) f-statistic
Slope (degrees)	4.3 ±5.3	6.8± 6.7	9.5 ±6.3	5.3 ±5.2	2.5 ±1.9	9.6 ±10.1	n/s	0.9	8.5***
Aspect (degrees)	215 ±112	193 ±127	103 ±93	93 ±79	212 ±51	200 ±135	n/s	1.2	1.6
Soil depth (mm)	341 ±145	269 ±169	244 ±130	252 ±147	159 ±51	494 ±401	n/s	0.6	1.2
Soil texture (% volume)									
Clay	4.7 ±1.2	4.9 ±0.9	4.5 ±1.6	5.5 ±1.7	4.7 ±1.0	4.7 ±1.2	n/s	0.7	0.9
Silt	5.8 ±2.5^{ab}	6.4 ±2.3^{a}	5.4 ±18^{ab}	6.2 ±1.5^{ab}	5.9 ±1.4^{ab}	3.9 ±1.3^{b}	13.0*	2.4	1.6
Fine sand	40.6 ±8.2^{a}	36.2 ±6.7^{ab}	31.7 ±4.4^{ab}	33.4 ±6.5^{ab}	33.3 ±3.0^{ab}	29.0 ±6.7^{b}	16.9**	5.5***	2.7*
Medium sand	28.7 ±15.7^{b}	22.4 ±2.5^{b}	24.5 ±3.8^{ab}	24.2 ±4.4^{ab}	29.1 ±4.5^{a}	26.9 ±3.7^{ab}	18.0**	0.6	0.9
Coarse sand	19.8 ±9.7^{b}	30.2 ±7.3^{ab}	33.9 ±6.5^{ab}	30.6 ±10.2^{ab}	26.9 ±3.8^{ab}	35.6 ±8.7^{a}	18.1**	0.9	0.6
Stone	4.4 ±3.2^{b}	6.2 ±3.2^{ab}	6.5 ±5.1^{ab}	4.8 ±3.9^{b}	6.9 ±2.5^{ab}	10.3 ±4.8^{a}	16.2**	4.5**	2.4*
Rock cover (%)	11.8 ±12.9	16.6 ±18.3	9.4 ±5.9	24.5 ±12.3	25.2 ±16.1	28.9 ±30.8	n/s	2.5	3.0*

Table 3.4 b Means (±SD) of physical soil properties for lowland habitat types in each vegetation type in a west-east gradient across the Kamiesberg. Significance levels are shown as: * = $p < 0.05$; ** = $p < 0.005$; *** = $p < 0.001$ (n = 6, no values are given for Mountain shrubland which does not have a lowland component). Post-hoc variation between vegetation types is indicated in superscript above each variable.

	Heuweltjieveld	Western klipkoppe	Mountain shrubland	Renosterveld	Eastern klipkoppe	Bushmanland ecotone	H-statistic and significance level
Slope (degrees)	0.0 ±0.0	1.0 ±0.0		0.5 ±0.8	0.9 ±0.6	2.9 ±9.7	n/s
Aspect (degrees)	198 ±155	111 ±121		76 ±88	155 ±112	206 ±147	n/s
Soil depth (mm)	305 ±114^{ab}	345 ±175^{ab}		367 ±127^{ab}	160 ±40^{b}	863 ±159^{a}	20.6***
Soil texture (% volume)							
Clay	5.0 ±1.1	5.0 ±1.3		5.7 ±2.1	5.2 ±1.2	4.2 ±1.3	n/s
Silt	6.5 ±1.2^{a}	6.0 ±2.1^{ab}		6.1 ±1.8^{a}	5.8 ±1.7^{ab}	4.7 ±1.2^{b}	13.7**
Fine sand	44.4 ±8.6^{a}	39.0 ±4.7^{a}		34.4 ±7.0^{ab}	34.4 ±2.6^{ab}	25.1 ±7.1^{b}	16.5**
Medium sand	22.3 ±1.9	22.0 ±2.7		24.6 ±3.0	25.3 ±1.6	28.4 ±4.4	n/s
Coarse sand	20.8 ±7.7^{b}	28.1 ±6.7^{ab}		29.1 ±10.4^{ab}	29.1 ±3.2^{ab}	39.1 ±10.5^{a}	11.3*
Stone	4.5 ±2.7^{ab}	3.8 ±1.6^{ab}		3.3 ±0.8^{b}	7.5 ±2.1^{a}	9.0 ±5.0^{a}	16.3**
Rock cover (%)	0.0 ±0.0^{b}	0.8 ±1.0^{bc}		13.4 ±3.4^{a}	10.5 ±3.3^{ac}	0.1 ±0.1^{b}	24.4***

Table 3.4 c Means (±SD) of physical soil properties for upland habitat types in each vegetation type in a west-east gradient across the Kamiesberg. Significance levels are shown as: * = $p < 0.05$; ** = $p < 0.005$; *** = $p < 0.001$ (n = 6). Post-hoc variation between vegetation types is indicated in superscript above each variable.

	Heuweltjieveld	Western klipkoppe	Mountain shrubland	Renosterveld	Eastern klipkoppe	Bushmanland ecotone	H-statistic and significance level
Slope (degrees)	8.4 ±4.4^{ab}	12.6 ±4.2^{ab}	9.5 ±6.3^{ab}	10.0 ±2.3^{ab}	4.2 ±1.3^{b}	15.2 ±17.5^{a}	13.4*
Aspect (degrees)	233 ±54	275 ±69	103 ±93	111 ±73	270 ±136	193 ±135	n/s
Soil depth (mm)	310 ±115^{a}	192 ±102^{ab}	244 ±130^{ab}	137 ±15^{ab}	159 ±63^{ab}	126 ±55^{b}	12.5*
Soil texture (% volume)							
Clay	4.4 ±1.3	4.9 ±0.6	4.5 ±1.6	5.4 ±1.5	4.3 ±0.7	5.1 ±1.0	n/s
Silt	5.0 ±3.3	6.8 ±2.5	6.2 ±1.4	6.0 ±1.3	3.2 ±0.9	5.6 ±2.0	n/s
Fine sand	36.8 ±6.2	33.4 ±7.6	31.7 ±4.4	32.5 ±6.5	32.1 ±3.1	32.8 ±3.5	n/s
Medium sand	35.0 ±21.0^{ab}	22.8 ±2.5^{b}	24.5 ±3.8^{ab}	23.8 ±5.8^{ab}	32.9 ±2.6^{a}	25.5 ±2.4^{ab}	12.1*
Coarse sand	18.8 ±12.1	32.2 ±7.8	33.9 ±6.5	32.3 ±11.0	24.7 ±3.2	32.0 ±5.0	n/s
Stone	4.3 ±4.0	8.5 ±2.4	6.5 ±5.1	6.3 ±5.2	6.3 ±2.9	11.5 ±4.7	n/s
Rock cover (%)	23.7 ±5.2^{bc}	32.3 ±11.9^{ab}	9.4 ±5.9^{b}	35.5 ±5.4^{ab}	39.9 ±6.3^{ac}	57.8 ±9.3^{a}	27.8***

Table 3.5.a Means (±SD) of chemical soil properties for combined upland and lowland habitat types in each vegetation type in a west-east gradient across the Kamiesberg. Significance levels are shown as: * = p < 0.05; ** = p < 0.005; *** = p < 0.001 (n = 12, except for Mountain shrubland where n = 6). Results of the nested-ANOVA are presented in the last two columns.

	Heuweltjieveld	Western klipkoppe	Mountain shrubland	Renosterveld	Eastern klipkoppe	Bushmanland ecotone	H-statistic and significance level	Vegetation f-statistic	Vegetation x (habitat type) f-statistic
pH (KCl)	6.2± 0.8^{ac}	6.2 ±1.1^{a}	4.6 ±0.6^{b}	5.0 ±0.7^{bc}	5.3 ±0.9^{ab}	6.2 ±0.6^{a}	24.5***	6.5***	2.9*
Resistance (ohms)	756 ±764^{b}	1873 ±2064^{bc}	4380 ±1128^{ac}	3785 ±1649^{ac}	3721 ±1314^{ac}	4228 ±2105^{a}	31.5***	15.3***	3.1*
Potassium (mg/kg)	166 ±96^{a}	139.1 ±78.9^{ab}	58.5 ±17.1^{b}	98.3 ±43.2^{ab}	96.5 ±43.7^{ab}	134.9 ±81.8^{ab}	12.2*	1.7	2.0
Phosphorus (mg/kg)	48.0 ±33.3	41.7 ±27.4	17.5 ±9.8	71.5 ±64.6	38.0 ±36.7	57.0 ±65.8	n/s	1.2	4.9***
Exchangeable cations (cmol(+)/kg)									
Sodium	0.65 ±0.58^{a}	0.5 ±0.7^{ac}	0.04 ±0.01^{bc}	0.08 ±0.04^{ab}	0.12 ±0.08^{ac}	0.03 ±0.02^{b}	34.9***	7.7***	1.2
Potassium	0.43 ±0.23^{a}	0.36 ±0.20^{ab}	0.15 ±0.04^{b}	0.25 ±0.11^{ab}	0.25 ±0.11^{ab}	0.35 ±0.21^{ab}	12.0*	1.7	2.1
Calcium	3.6 0±2.70	3.41 ±2.83	1.72 ±1.13	2.62 ±1.12	1.51 ±0.70	2.38 ±2.57	n/s	3.2*	2.6*
Magnesium	1.76 ±0.73^{a}	1.53 ±1.06^{ac}	0.42 ±0.12^{b}	1.07 ±0.48^{ab}	1.18 ±0.55^{ab}	0.82 ±0.64^{bc}	20.5**	3.8*	2.1
Nitrogen (vol %)	0.07 ±0.02^{ac}	0.06 ±0.03^{ab}	0.08 ±0.04^{ab}	0.08 ±0.07^{a}	0.04 ±0.01^{bc}	0.03 ±0.02^{b}	27.7**	7.1***	5.5***
Carbon (vol %)	0.86 ±0.41^{a}	0. 26 ±0.41^{ab}	0.85 ±0.64^{a}	1.32 ±1.00^{a}	0.43 ±0.19^{b}	0.40 ±0.35^{b}	23.2**	14.5***	9.6***

Table 3.5 b Means (±SD) of chemical soil properties for lowland habitat types in each vegetation type in a west-east gradient across the Kamiesberg. Significance levels are shown as: * = p < 0.05; ** = p < 0.005; *** = p < 0.001 (n = 6, no values are shown for Mountain shrubland as it does not have a lowland component). Post-hoc variation between vegetation types is indicated in superscript above each variable.

	Heuweltjieveld	Western klipkoppe	Mountain shrubland	Renosterveld	Eastern klipkoppe	Bushmanland ecotone	H-statistic and significance level
pH (KCl)	6.3 ±1.1	6.0 ±1.1		5.3 ±0.7	6.0 ±0.6	6.4 ±0.7	n/s
Resistance (ohms)	610 ±715^{b}	2646 ±2697^{ab}		2725 ±1612^{ab}	3878 ±795^{ab}	5643 ±1287^{a}	17.8**
Potassium (mg/kg)	160.3 ±74.0	157.2 ±81.3		88.7 ±36.3	118.0 ±31.1	83.5 ±32.2	n/s
Phosphorus (mg/kg)	23.3 ±16.5	31.6 ±16.8		42.0 ±22.8	58.3 ±43.9	28.2 ±14.8	n/s
Exchangeable cations (cmol(+)/kg)							
Sodium	0.89 ±0.66^{a}	0.77 ±1.05^{a}		0.11 ±0.03^{ab}	0.12 ±0.08^{ab}	0.02 ±0.01^{b}	16.9**
Potassium	0.41 ±0.1	0.40 ±0.20		0.22 ±0.09	0.30 ±0.08	0.21 ±0.08	n/s
Calcium	2.87 ±1.97	2.49 ±1.87		2.55 ±1.05	1.61 ±0.37	1.05 ±0.36	n/s
Magnesium	1.72 ±0.56^{a}	1.57 ±1.40^{ab}		1.38 ±0.43^{ab}	1.37 ±0.42^{ab}	0.51 ±0.20^{b}	11.7*
Nitrogen (vol %)	0.05 ±0.01^{a}	0.04 ±0.01^{ab}		0.05 ±0.01^{a}	0.03 ±0.00^{ab}	0.02 ±0.00^{b}	20.5***
Carbon (vol %)	0.59 ±0.16^{a}	0.40 ±0.28^{ab}		0.63 ±0.20^{a}	0.34 ±0.10^{ab}	0.21 ±0.03^{b}	17.5**

Table 3.5 c Means (±SD) of chemical soil properties for upland habitat types in each vegetation type in a west-east gradient across the Kamiesberg. Significance levels are shown as: * = p < 0.05; ** = p < 0.005; *** = p < 0.001 (n = 6). Post-hoc variation between vegetation types is indicated in superscript above each variable.

	Heuweltjieveld	Western klipkoppe	Mountain shrubland	Renosterveld	Eastern klipkoppe	Bushmanland ecotone	H-statistic and significance level
pH (KCl)	6.0 ±0.5^{ab}	6.3 ±1.1^{ab}	4.6 ±0.6^{b}	4.7 ±0.4^{b}	4.7 ±0.6^{b}	5.9 ±0.3^{a}	23.7***
Resistance (ohms)	903 ±849^{b}	1100 ±815^{b}	4380 ±1128^{a}	4846 ±828^{a}	3565 ±1763^{ab}	2813 ±1814^{ab}	23.0***
Potassium (mg/kg)	173.0 ±121.6	121.2 ±79.5	58.5 ±17.1	107.5 ±50.9	75.2 ±46.2	186.3 ±85.7	n/s
Phosphorus (mg/kg)	73.3 ±25.6^{a}	51.8 ±33.6^{ab}	17.5 ±9.8^{b}	101.0 ±81.2^{ab}	17.6 ±7.5^{b}	86.0 ±85.4^{ab}	18.4**
Exchangeable cations (cmol(+)/kg)							
Sodium	0.42 ±0.42^{a}	0.23 ±0.17^{ab}	0.04 ±0.01^{a}	0.05 ±0.02^{ab}	0.11 ±0.07^{ab}	0.04 ±0.02^{b}	15.7**
Potassium	0.44 ±0.31	0.31 ±0.20	0.15 ±0.04	0.28 ±0.13	0.19 ±0.12	0.47 ±0.21	n/s
Calcium	4.31 ±3.28	4.33 ±3.49	1.72 ±1.13	2.68 ± 1.28	1.41 ±0.95	3.70 ±3.19	n/s
Magnesium	1.79 ±0.93^{a}	1.49 ±0.69^{a}	0.42 ±0.12^{b}	0.76 ±0.28^{ab}	0.99 ±0.63^{ab}	1.14 ±0.79^{ab}	13.8*
Nitrogen (vol %)	0.08 ±0.02	0.08 ±0.03	0.08 ±0.04	0.12 ±0.08	0.04 ±0.01	0.04 ±0.03	n/s
Carbon (vol %)	1.14 ±0.41^{ab}	0.83 ±0.42^{ab}	0.85 ±0.64^{ab}	2.01 ±1.01^{a}	0.52 ±0.22^{b}	0.61 ±0.43^{b}	15.9**

3.3.3. Habitat considerations

Upland habitats across the Kamiesberg are differentiated from lowland habitats where they have steeper slopes, shallower soils, and higher percentage rock cover (Table 3.6). Upland soils are also consistently more acidic with higher soil nitrogen and carbon. Within vegetation types, habitats vary significantly with regard to slope, percentage fine sand, rockiness and rock cover. In terms of soil chemistry, upland habitats also vary significantly from lowland habitats with regards to pH, exchangeable calcium, and percentage carbon and percentage nitrogen.

Table 3.6 Means (±SD) of abiotic variables for grouped lowland and upland habitats across the entire Kamiesberg mountain range (lowlands n = 33, uplands n = 30). Statistics are Mann-Whitney-U z-scores, and significance levels are shown as: * = $p < 0.05$; ** = $p < 0.001$.

Variable	Lowlands	Uplands	z-scores
Slope (degrees)	1 ±4	10 ±6	-6.45**
Aspect (degrees)	148 ±128	197 ±115	ns
Soil depth (mm)	408 ±271	206 ±129	3.72**
Soil texture (% volume)			
Clay	5.0 ±1.4	4.8 ±1.1	ns
Silt	5.6 ±1.8	5.6 ±2.1	ns
Fine sand	35.4 ±8.7	33.2 ±5.3	ns
Medium sand	24.5 ±3.6	27.4 ±9.8	ns
Coarse sand	29.2 ±9.6	28.9 ±9.4	ns
Stone	5.6 ±3.4	7.3 ±4.5	ns
Rock cover (%)	4.9 ±6.2	33.1 ±16.1	2.82**
pH (KCl)	6.0 ±0.8	5.4 ±1.0	2.32*
Resistance (ohms)	3100 ±2236	2934 ±1932	ns
Potassium (mg/kg)	121.5 ±61.4	120.2 ±83.8	ns
Phosphorus (mg/kg)	36.7 ±26.7	57.8 ±57.6	ns
Exchangeable cations (cmol(+)/kg)			
Sodium	0.38 ±0.63	0.15 ±0.22	ns
Potassium	0.31 ±0.15	0.30 ±0.21	ns
Calcium	2.11 ±1.42	3.02 ±2.61	ns
Magnesium	1.33 ±0.80	1.14 ±0.75	ns
Nitrogen (vol %)	0.03 ±0.02	0.07 ±0.05	-3.88**
Carbon (vol %)	0.44 ±0.22	0.99 ±0.74	-4.11**

Growth form and substrate relationships examined at high altitude sites showed a strong positive relationship between percentage succulent cover and rock cover ($n = 270$, $H = 170.36$, $p < 0.001$) and similarly between woody perennials and bare ground ($n= 270$, $H = 181.65$, $p < 0.001$).

3.4 DISCUSSION

3.4.1 Emerging ecoregions

On the basis of this characterisation the Kamiesberg mountain range can be broadly divided into what are termed the western, upper and eastern ecoregions. An ecoregion is defined as a large unit of land within which there is relative similarity in the mosaic of ecosystems and ecosystem components. These components give recognition to a geographically distinct assemblage of species or natural communities and environmental conditions, the boundaries of which encompass ecological and evolutionary processes (Burgess et al., 2005). Climatic factors, soil texture and soil chemistry vary considerably across the range, and are strong determinants of these three distinct ecoregions. While these ecoregions are robust and supported by both floristic and abiotic environmental variables, they are not always clearly delimited. The western component comprises the Heuweltjieveld and Western klipkoppe, the upper component the Renosterveld and the eastern component the Bushmanland ecotone. Mountain shrubland and Eastern klipkoppe group with either their western or eastern neighbours depending on the variables under consideration. Upland and lowland habitats are shown to share some consistent elements across the entire mountain range, confirming their status as characteristic of the landscape mosaic that comprises the Kamiesberg (Adamson, 1938). These habitats are also shown to vary subtly in conjunction with each vegetation type, contributing to the landscape heterogeneity of the area. The three broad ecoregions suggested in this study, and the constituent vegetation types, and the role of habitat within the broader landscape and within vegetation types, are considered in detail below.

3.4.2 Landscape-scale boundaries: ecoregions and constituent vegetation types

The suggested western ecoregion, comprising the Heuweltjieveld and Western klipkoppe is relatively climatically more temperate due to the moderating influence of the Atlantic Ocean (Desmet and Cowling, 1999b). The aeolian sands and the proximity of the coastal forelands to the ocean make the soils on these western and lower slopes considerably higher in sodium and this region has characteristically fine, saline soils (Lloyd, 1989a; Watkeys, 1999; Francis et al., 2007). Heuweltjieveld and Western klipkoppe are both largely dominated by succulents and to a lesser degree by annuals and geophytes, and in the case of Western klipkoppe, by dwarf woody shrubs as well. This high degree of succulence is attributed to both the more temperate nature of the climate on the western side of the Kamiesberg and the close relationship between succulence and saline soils (Lloyd, 1989a; Milton et al., 1997; Watkeys, 1999; Francis et al., 2007). A further factor possibly contributing to this predominance of succulents is that following rainfall, water does not penetrate very deeply in these finer textured soils and this favours the typically shallow rooted Mesembryanthemaceae, which are the dominant succulents in this system (Noy-Meir, 1973; Eccles et al., 1999). These vegetation types share several common and dominant species, and *Galenia sarcophylla* and *Zygophyllum morgsana* are ubiquitous.

This study based its vegetation types to a large extent on those of Mucina and Rutherford (2006), and finds strong support for their recognition of the Heuweltjieveld as a distinct vegetation type. This study shows that the Heuweltjieveld has a higher general plant cover and is almost singularly dominated by succulent shrubs while the Western klipkoppe has a greater mix of succulent and woody shrubs. While most authors do not treat these vegetation types as separate, Mucina and Rutherford (2006) term the Western klipkoppe lowlands 'Blomveld'. This current study did not find this vegetation type dominated by annuals as this name implies. This is attributed to the relatively low rainfall year in which sampling was carried out, the avoidance of old and currently cultivated fields where annuals predominate, and the highly patchy nature of annuals (Mucina and Rutherford, 2006). Other authors have drawn the line between vegetation types on the western slopes of the Kamiesberg between what are termed here the Western klipkoppe lowlands and Western klipkoppe uplands (Acocks, 1952; Low and Rebelo, 1996).

Adamson (1938) commented on the lack of a sharp boundary marking the base of the Kamiesberg, where other karoo mountains have a more marked beginning and end point. This study supports this view as no one point signals the start of the Kamiesberg proper. With the granitic intrusions interspersed with the sandy lowland areas, at variable altitudes, a mosaic of distinctive vegetation types emerges, but no clear boundary exists between the coastal and mountain environments.

The position of the Mountain shrubland on the western slopes of the Kamiesberg suggests that it benefits from both the influence of orographic rainfall, as well as from the relatively more moderate climatic conditions associated with this western, seaward-facing aspect where winter temperature ranges are less extreme and frost days less common than to the east. The soils, which are different to those of the western and eastern neighbouring vegetation types, are deep with little rock cover. They are also acidic, possibly due to leaching from more available water. This in turn may account for the lower exchangeable cations available in these soils (Kamprath, 2000). The Mountain shrubland community comprises a major shift away from Mesembryanthemaceae dominated succulent shrublands, to a taller woody shrubland of higher cover and larger plants, and is host to the few tree species recorded in this study, such as *Dodonea viscosa* and *Ficus ilicina*. In keeping with the Western klipkoppe uplands, the Mountain shrublands have a relatively high cover of annual grass which may be a function of the moderate climatic conditions and some restriction of grazing as a result of inaccessibility due to slope or the dense plant cover (Petersen et al., 2004). Shared elements are also evident in the woody shrub *Lebeckia multiflora*, which is common across both Mountain shrubland and Western klipkoppe uplands.

The climate regime associated with Mountain shrubland could reduce this vegetation type to a transitional or 'ecotonal' vegetation type between the western and upper ecoregions. However, a sharp boundary in salinity is evident to the west and Mountain shrubland soils are more similar to adjacent Renosterveld soils. Vegetation structure also more closely aligns the Mountain shrubland with the upper ecoregion, where the higher rainfall at these altitudes results in significantly greater cover in woody shrubs (Schultze et al., 1996). Despite links to Western klipkoppe and Renosterveld, in

keeping with previous authors, this study makes a case for Mountain shrubland as a distinct vegetation type. The unique combination of aspect and climate and associated weathering has resulted in less rocky and chemically distinct soils with an associated vegetation type of high cover of tall woody shrub and tree species. The findings of this study are in agreement with Adamson (1938) who noted a 'west facing escarpment slope community' and with Mucina and Rutherford (2006) who also recognise Mountain shrubland as a distinct vegetation type, which they term 'Kamiesberg Mountain Shrubland'.

With water as a primary factor controlling plant growth and distribution, especially in arid and semi-arid areas, the rainfall gradient across the Kamiesberg is tracked by greater cover and structurally larger plants with increased water availability at altitude (Noy-Meir, 1973; Rutherford, 1980; Abd el-Ghani and Amer, 2003). The upper ecoregion, which is defined by Renosterveld, is characterised by these elements of higher plant cover and larger and woodier shrub species. Renosterveld, a more widely recognised vegetation type characterised by 'renosterbos' or *Elytropappus rhinocerotis*, from the cooler climates to the south, is a relic from a cooler climatic era and persists at the top of the Kamiesberg under the favourable climatic conditions of higher rainfall and cooler temperatures (Adamson, 1938; Low and Rebelo, 1996). *Elytropappus rhinocerotis* dominates the lowland areas where soils are deeper and occurs on the fringes of the upland areas in characteristic association with the tall bunch grass *Merxmuellera stricta* (Manning and Goldblatt, 1997). These upper ecoregion sites are characterised by high soil carbon and nitrogen, a function of the higher plant cover, especially of perennial woody species which dominate here (Flombaum and Sala, 2007). Larger shrubs generate more litter and serve to trap wind-blown sand and litter. Grazers are also limited by the generally steep slopes in this ecoregion and dense cover changes the local soil environment. All these factors serve to promote biomass and an increase in plant cover (Noy-Meir, 1973; Feral et al., 2003).

While the soils of this upper ecoregion vary from surrounding soils, in terms of textural and chemical constituents, succulents are not excluded on this basis. Some succulents persist at these higher altitudes, although they occur predominantly in association with the large areas of exposed granite. This study suggests that either fire

or interspecific competition limits and restricts succulents at the top of the Kamiesberg. The idea that overgrazing within the Renosterveld increases the karoo elements in this vegetation type would point towards an argument in favour of competition (Mucina and Rutherford, 2006) (see also Chapter 5). Carrick (2003) found evidence of intraspecific and interspecific competition between succulent Mesembryanthemaceae shrubs, but limited interspecific competition between these shrubs and an adjacent non-succulent shrub on the basis of variable rooting depths (Carrick, 2003). Shiponeni (2007) also showed the importance of variable rooting depth in allowing co-existence in otherwise highly competitive grass and succulent shrubs in the Bushmanland ecotone. This, in conjunction with the fact that succulents in the upper ecoregion are more inclined to occupy the niche presented by rocky outcrops, suggests that those succulents that can grow at these altitudes persist in fire refugia, as demonstrated in other fire-prone systems (Thomas and Goodson, 1992). The question of what drives this interface between woody-shrub dominated vegetation and adjacent succulent dominated vegetation is a microcosm of the greater question around boundaries between the Succulent Karoo and Fynbos biomes, which Aggenbag (2004) similarly attributes to competition or fire (Aggenbag et al., 2004). Lechmere-Oertel and Cowling (2001) more specifically suggest that the boundaries of the Fynbos biome are limited by water and the Succulent Karoo biome boundaries are limited by plant interactions (Esler, 1993; Lechmere-Oertel and Cowling, 2001).

Contrary to more recent mapping efforts, which tend to group western and eastern vegetation types across the Kamiesberg, Adamson (1938) notes how different the vegetation is on the eastern and western aspects of the mountain. While there are undoubted similarities, compositionally the eastern and western vegetation types are unique. The Western and Eastern klipkoppe share a general plant structure, with a mix of woody shrubs and succulents. However, while these two vegetation types share several species, the dominant and most common species differ considerably between them. For example, to the west are species such as *Lycium ferocissimum*, *Aridaria serotina* and *Ruschia macownii*, and to the east *Eriocephalus ericoides*, *Ruschia robusta* and *Cheiridopsis denticulata*. The major abiotic difference is the climatic variation, where temperatures in the Eastern klipkoppe are more extreme and frost a relatively frequent occurrence, aligning this vegetation type more closely with Renosterveld, in the upper ecoregion. However, seasonal temperature ranges and the

mean number of frost days experienced in a year also group the Eastern klipkoppe with the extreme eastern Bushmanland ecotone. Despite cover and growth form similarities with Renosterveld, on floristic grounds the Eastern klipkoppe clusters more closely with Bushmanland ecotone sites than Renosterveld sites to the west. As with Mountain shrubland, there may be an argument for an 'ecotonal' vegetation type between the greater upper and eastern ecoregions. However, Eastern klipkoppe is undoubtedly not Resnosterveld as it lacks the dominant *Elytropappus rhinocerotus*. It also does not have the grassland elements that are characteristic of the Bushmanland ecotone, and as argued above it is not simply an extension of the Western klipkoppe. Although the Eastern klipkoppe may sit between the upper and eastern ecoregions, it comprises a distinct succulent and woody shrub mix, on acid soils and experiences a more extreme climate with numerous frost days. It therefore warrants its own place in the continuum of vegetation types across the Kamiesberg.

The eastern ecoregion is defined by the Bushmanland ecotone vegetation type. The Bushmanland ecotone is determined by both substrate and climate (Shiponeni, 2007). The climate is characterised by low rainfall, with limited winter rainfall reaching so far east, and erratic summer rainfall, as well as more marked temperature extremes. The soils also differ chemically from surrounding soils, further separating out this group. This can be attributed to different parent material, where these soils are largely aeolian in origin, while neighbouring soils are formed *in situ* (Lloyd, 1989a). Infiltration is more rapid in these coarse soils, allowing deeper penetration of limited and sporadic rainfall events (Noy-Meir, 1973; Montana et al., 1990). There is a typical increase in grasslands with the progression east and the beginning of the summer rainfall regime (Hilton-Taylor, 1996; Shiponeni, 2007). The perennial grasslands require these deeper, coarse soils, and *Stipagrostis brevifolia* is particularly able to cope with infrequent rainfall. The prevalence of annuals is further testimony to the low and irregular nature of the rainfall (Lloyd, 1989b). One might expect the Bushmanland ecotone uplands to be a continuation of the rocky hills to the west, but these are environmentally and florally distinct. These uplands are particularly steep and rocky and this topography must concentrate sufficient water to sustain the higher number of woody shrubs here (Ludwig, 1987). Griqualand West and Bushmanland is a recognised subdivision of the Nama-karoo biome, and the inclusion of this ecotonal region in this study may be debatable (Palmer and Hoffman, 1997). However, the

boundaries between the Succulent Karoo and Nama-karoo are described as 'fluid and blurred', and a number of common elements are evident such as *Eriocephalus ericoides*, *Euphorbia decussata* and *Rhynchopsidium pumilum* between the Bushmanland ecotone and adjacent Eastern klipkoppe (Milton et al., 1997). As the focus of this characterisation is on drivers of transition, the inclusion of this ecotonal vegetation type has proved informative.

3.4.3 Landscape-scale boundaries: upland and lowland habitats

Habitats within vegetation types typically differ on the basis of slope and rock cover which is readily anticipated due to characteristic topographic variations. Upland habitats also have higher carbon and nitrogen. Higher soil phosphorus in these rocky upland sites is explained by the close association between soil phosphorus and parent material and the extent of pedogenesis which is recent in these rocky upland habitats (Kamprath, 2000). Higher soil carbon and nitrogen may be attributed to greater woody biomass on these upland sites (Flombaum and Sala, 2007). In semi-arid areas local topography is vital in determining water distribution (Ludwig, 1987). In the Kamiesberg rocky upland habitats this translates into structurally taller and frequently woodier vegetation, greater canopy area, more plant litter, and faster decomposition in response to higher soil moisture (Noy-Meir, 1973; Milton, 1990b; Aguilera et al., 1999; Abd el-Ghani and Amer, 2003). Greater organic matter may also be allowed to accumulate as these rocky upland habitats are less frequently, and less intensely, grazed than lowland habitats (Petersen et al., 2004; Anderson and Hoffman, 2007). This local topographic diversity frequently translates into higher species diversity, and this is evident in most vegetation types investigated in this study (Cowling et al., 1994; Abd el-Ghani and Amer, 2003).

3.4.4 Landscape-scale boundaries: in conclusion

What emerges from this characterisation of the selected vegetation types is the suggestion of a broad landscape-scale division of the Kamiesberg into three ecoregions, based on climatic, soil texture and soil chemistry gradients. A region of textually fine and saline soils with a climate of little rainfall, extreme seasonal temperatures but very few frost days, dominated by succulents, comprises the western ecoregion. A relatively wetter climate, with cooler seasonal temperatures, with a high incidence of frost, with acidic soils with high nitrogen and carbon content and with

high plant cover in particular of larger woody species, forms the upper ecoregion. A more arid region with very low and highly variable rainfall, and greater extremes in seasonal temperatures with cool winter temperatures with some frost days and hotter summer maximum temperatures, with coarse soils and communities dominated by a mix of shrubs and succulents, with the emergence of Bushmanland perennial grass, forms the eastern ecoregion. These driving factors do not act in a synchronised and uniform manner, but rather in more subtle combinations and gradations, which give rise to the distinct vegetation types evident across the range. A further gradient in operation across the Kamiesberg is that of habitat, where upland and lowland habitats share some consistent elements and in other regards are influenced by the unique nature of each vegetation type. The role of individual plants, though not explicitly examined here, cannot be overlooked. Niche theory tells us that species will flourish at their optimum niche along an environmental gradient of abiotic and biotic factors (Beals, 1969). Biotic interactions in the form of competition between species can generate sharp boundaries between vegetation types (Beals, 1969). Abiotic gradients may vary seasonally and are affected by subtle combinations of topography and aspect. Species respond to these factors and to each other, tolerating regional co-existences or causing local exclusions through competitive interactions over resources (Czaran, 1991). These factors give rise to vegetation types, more or less cohesive, with shifting or grading boundaries. Indeed, most authors of vegetation maps will acknowledge that prescribing vegetation boundaries is difficult, and often a function of scale of interest.

3.4.5 The potential impact of environmental change

If the current environmental gradient is viewed in light of proposed climate change for the region, we may anticipate a retreating of vegetation up the Kamiesberg in response to reduced winter rainfall (MacKellar et al., 2007). However, the evidently important role of soil texture and chemistry gradients could limit movement of certain vegetation types and act as a barrier to immigration by others. For example, species favoured by the more sodium-rich soils in the western ecoregion may not tolerate the more acid soils of their up-slope neighbouring vegetation type, Mountain shrubland. In the eastern ecoregion, where proposed increased summer rainfall could potentially allow the expansion of the *Stipagrostis brevifolia* grasslands however, this study suggests these are limited in turn by soil textural requirements. These *S. brevifolia*

grasslands are unique in their ability to tolerate very low rainfall and may find themselves facing new competitive threats from other grasses such as *S. ciliata* which are currently limited in this area by low rainfall (Lloyd, 1989a) or from shrubs such as *Ruschia robusta* (Shiponeni, 2007).

Increased incidence of drought may also increase fire frequency in the Renosterveld, with unknown consequences. Based on these considerations, the predicted 40% loss of the current bioclimatic envelope for the Succulent Karoo biome by 2050 can be readily imagined (Midgley and Thuiller, 2007). However, the findings of previous studies, suggest that plants possess a variable response to environmental change and that this is dependent on each plant's ecophysiology (Midgley and Thuiller, 2007). Modelling studies also suggest the important role of microhabitats, which are common in the Kamiesberg, in the maintenance of species in the face of change (Frank and McNaughton, 1991; Midgley and Thuiller, 2007). However, in demonstrating the subtle differences in habitats across the Kamiesberg, this study suggests that the upland habitats cannot be assumed to act as general refugia for all plant species. While this current study cannot elucidate plant responses, it does provide a better understanding of the environmental factors characterising communities and determining vegetation distribution across the Kamiesberg, notably the importance of both climate and soil factors, and serves as a useful starting point to further studies in this area. In his description of the vegetation of the Kamiesberg, Adamson (1938) notes that, "the vegetation … shows an exceedingly close correlation with climate and habitat conditions", and this study corroborates this.

4. AN EXAMINATION OF THE IMPACTS OF SUSTAINED HEAVY GRAZING ON PLANT DIVERSITY AND COMPOSITION IN LOWLAND AND UPLAND HABITATS ACROSS THE KAMIESBERG USING A SIMPLE GROWTH-FORM ANALYSIS

Abstract: This chapter explores the impacts of sustained heavy grazing in the six vegetation types across the altitudinal and rainfall gradient in the Kamiesberg. The study was carried out across the fence separating the Leliefontein communal area and surrounding privately-owned farms. The communal area has been stocked over decades at approximately twice the government recommended stocking rate, while adjacent privately-owned farms have generally adhered to recommended rates. Plant community data were collected from 66, 0.1 ha modified Whittaker plots and analysed for diversity and compositional changes. Consideration of community-wide responses through non-metric multidimensional scaling (NMDS) ordination showed that heavy grazing did not result in the dominance of a few wide-spread, weedy species in communal areas. Species richness at the 0.1 ha scale was also not affected by different land use practices. However, there was a significant compositional shift away from large woody and succulent shrubs, and an associated increase in dwarf shrubs and herbaceous perennial plants on the communal areas. This shift was only evident on the sandy lowland habitats, while a reduction in perennial grass was recorded in the rocky upland habitats of the communal areas. Compositional shifts towards smaller and more ephemeral species in the communal area are indicative of a system more closely dependent on rainfall. This density-dependent effect has implications for people's livelihoods in the region, particularly in light of predicted climate change.

4.1 INTRODUCTION

There has been much debate as to the effects of livestock grazing on plant communities. Some researchers suggest positive impacts, in particular in response to light grazing with reported increases in plant diversity (Naveh and Whittaker, 1980; Waser and Price, 1981; Ayyad and Elkadi, 1982; Noy-Meir et al., 1989; West, 1993), while others provide more substantial evidence of negative impacts (Waser and Price, 1981; Olsvig-Whittaker et al., 1993; Fleischner, 1994; Shaltout et al., 1996). The nature of these impacts vary, ranging from simple losses in cover (Brady et al., 1989; Shaltout et al., 1996; Eccard et al., 2000), to variations in general diversity (Ayyad and Elkadi, 1982; West, 1993), and to more specific compositional shifts. Reported compositional shifts are from systems dominated by plants with perennial life histories to plants with annual life histories(Ayyad and Elkadi, 1982; Noy-Meir et al., 1989; Olsvig-Whittaker et al., 1993; Steinschen et al., 1996; Todd and Hoffman,

1999), loss of perennial cover with increased geophyte cover (Noy-Meir and Oron, 2001), and to systems dominated by less palatable species in response to the selective pressure of grazing (West, 1993; James et al., 1999; Todd and Hoffman, 1999; Riginos and Hoffman, 2003). Such selective pressure can result in a loss of heterogeneity, as different vegetation types might become increasingly homogenous in composition and cover, where previously cover was divided between a variety of species it becomes dominated by a few unpalatable species (Hoffman and Cowling, 1990, 1991; James et al., 1999).

The role of variable habitats in limiting or influencing grazing impacts has also received attention. Rocky upland habitats are believed to be less targeted by grazers due to their inaccessible nature, and plant communities in these areas are therefore less likely to show grazing responses than equivalent lowland areas (Cowling et al., 1994; Todd and Hoffman, 1999; Riginos and Hoffman, 2003; Petersen et al., 2004; Pienaar et al., 2004).

Previous work exploring grazing impacts in Namaqualand showed a significant decrease in leaf succulents and woody shrubs, with an associated increase in annual and geophyte cover, in response to the sustained heavy grazing experienced on the communal areas (Todd and Hoffman, 1999). This work was geographically restricted to one area of Namaqualand, and without particular reference to habitat type. The role of habitat type in terms of grazing is of particular relevance in the Kamiesberg, which is a mosaic of flat, sandy, lowland habitats and immediately adjacent, rocky upland habitats. This chapter, which has the central aim of expanding our understanding of grazing impacts in semi-arid regions, addresses the following questions:

1. Does heavy grazing result in the loss of species richness across a region and the homogenisation of previously distinct vegetation types?
2. Does heavy continuous grazing on the communal areas result in a shift from larger plants with a perennial life history to smaller plants with an annual life-history?
3. Are rocky upland habitats buffered against grazing impacts due to their less accessible nature?

4.2 METHODS

This study was carried out across the boundary of the Leliefontein communal area and the surrounding, privately-owned farms. For study area details see Chapters 2 and 3.

4.2.1 Data collection

Abiotic and biotic data were collected as described in Chapter 3, with the exception that for each site laid out on the private rangeland, in this study a paired site was included on the adjacent communal rangeland. Sites were selected based on minimising geographic variability such as slope and aspect, and for accessibility.

Species sampled were assigned to one of the following life history and growth form categories: annual herbs, annual grasses, geophytes, perennial grasses, dwarf shrubs (including all perennials of less than 25 cm in height, and all perennial herbs), woody shrubs (including all woody shrubs of more than 25 cm in height), succulents (including both stem and leaf succulents), and trees.

In the absence of accurate stocking-rate data for each specific site, where paddock size, the seasonal movement of livestock, distance to watering points, and stock posts all vary and result in a patchy pattern of livestock grazing, a subjective grazing score was determined. This grazing score was set on a scale of one (heavily grazed) to five (no evidence of grazing). This was based purely on a visual assessment of grazing evidence and on the amount of dung, grazing-damaged shrubs, and extent of livestock footpaths.

4.2.2 Statistical analyses

A paired Wilcoxon sign-rank test was used to test for significant differences in abiotic variables and grazing score, species number, plant cover, and cover of the compositional growth forms, on either side of the fence.

PC-ORD was used for multivariate analyses of all plots sampled across the study area, and those within each vegetation type (McCune and Grace, 2002). To analyse the

interrelationships between taxa and the relationships between taxa and environmental features, non-metric multidimensional scaling (NMDS) and joint-plotting of environmental variables was used. While a detailed analysis of the role of abiotic drivers in determining vegetation types is presented in the previous chapter, Chapter 3, environmental factors were included here with the added dimension of a grazing score, to explore the relative roles of abiotic and biotic drivers. NMDS is described as most appropriate for biotic community data in that it can accommodate large numbers of zero values, carries no assumption of multivariate normality, and has been shown to produce the most accurate representation of underlying data structure (Clarke, 1993). Cover percentages were transformed using Beals smoothing and the analysis was run 300 times using random starting configurations (McCune and Grace, 2002). Pearson and Kendal correlations were calculated, and squared values used to express the proportion of variation in position accounted for by the variable in question (McCune and Grace, 2002). Mean axes positions and coeficient of variation scores were compared and Tukeys Honest Significant Difference host hoc analysis used to test for significant differences between communal and private sites in each vegetation type.

Single factor analysis of variance (ANOVA) for parametric data was used to test for significant differences in species richness for each cumulative area sampled, for lowland and upland areas respectively. In both the lowland and upland sites, data were non-normal for the 1 m^2 sample area. In each case a Mann-Whitney-U test for non-parametric data was used to test for significant differences.

4.3 RESULTS

4.3.1 Abiotic and grazing score

There were no significant differences in the measured abiotic variables across the fence in both lowland and upland sites (Table 4.1). In accordance with the mean stocking rates for the greater Leliefontein reserve (Todd and Hoffman, 2000) the mean grazing score was significantly higher on the communal area.

Table 4.1 The mean (±SD) plot values of the abiotic variables listed and the mean grazing score for each side of the fence separating communal areas and privately-owned farms in lowland and upland vegetation types in the Kamiesberg. The significance of across-fence differences were tested using a Wilcoxon matched pairs test; z scores and significance levels are given.

	Lowlands				Uplands			
	Communal	Private	z score	p (n = 30)	Communal	Private	z score	p (n = 36)
Soil depth (cm)	40.1 ± 26.8	41.1 ± 28.5	0.82	NS	21.1 ± 9.0	17.2 ± 10.4	1.63	NS
Slope (deg)	0.5 ± 0.5	2.1 ± 6.1	1.46	NS	8.8 ± 4.7	11.7 ± 6.4	1.66	NS
Stone content (%)	6.0 ± 4.3	5.3 ± 2.3	0.04	NS	6.8 ± 4.1	7.7 ± 5.0	0.89	NS
Rock cover (%)	5.5 ± 6.9	4.4 ± 5.5	1.48	NS	32.4 ± 17.7	33.7 ± 15.9	0.66	NS
Grazing score	3.5 ± 0.6	2.8 ± 0.7	2.62	0.008	2.9 ± 0.9	2.3 ± 0.6	3.17	0.002

4.3.2 Community response

The NMDS ordination diagram (Figure 4.1) of species cover data for all 66 plots shows plots arranged within discrete vegetation types irrespective of land use. Upland and lowland sites within a vegetation type were also rarely separated in ordination space. Pearson and Kendal correlations show median annual rainfall, the CV in median annual rainfall, and altitude as the most important environmental factors influencing the distribution of vegetation types in ordination space (Table 4.2). Table 4.3 presents the mean and coefficient of variation of axes 1 and 2 for communal and private sites in each vegetation type. Tukeys Honest Significance Difference post hoc test showed no significant variation between axes, as a reflection of ordination space, between communal and private sites in each vegetation type, while differences between vegetation types were consistently significant.

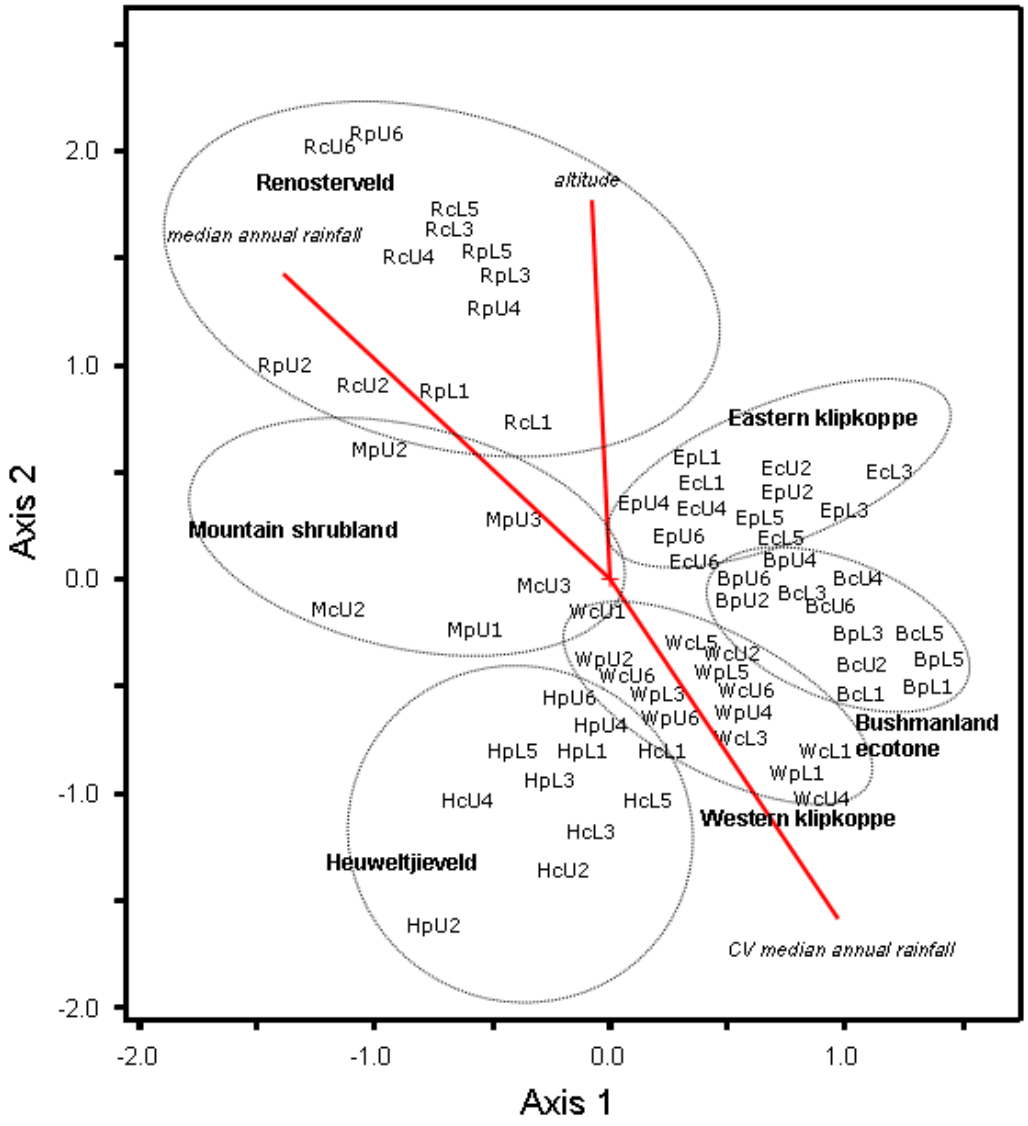


Figure 4.1 Nonmetric Multidimensional Scaling ordination of the plots sampled by species composition and cover, using Beals smoothing, with a biplot of abiotic factors (n = 66, r^2 axis 1 = 0.64, 2 = 0.23, stress = 13.79). Lowercase p and c stand for privately-owned farms and communal areas respectively, and uppercase U and L stand for upland and lowland habitats respectively. Sites are numbered according to their fence-line pairs.

Table 4.2 Pearson and Kendall correlations squared for abiotic variables with the ordination axes as presented in Figure 2 (n = 66). Significant values are shown as: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Variable	Axis 1 r^2	Axis 2 r^2
Altitude	0.7***	0.58***
Aspect	0.03	0.09*
Slope	0.01	0.00
Stone (%)	0.14**	0.01
Rock cover (%)	0.01	0.03
Grazing score	0.01	0.18**
Median annual rainfall	0.04	0.82***
Coefficient of variation in median annual rainfall	0.00	0.80***

Table 4.3 Mean and coefficient of variation (CV) scores for axes 1 and 2 for communal and private sites in each vegetation type as presented in Figure 4.1. (HV = Heuweltjieveld, WK = Western klipkoppe, MS = Mountain shrubland, RV = Renosterveld, EK = Eastern klipkoppe, BE = Bushmanland ecotone). Tukey's Honest Significant Differences post-hoc analysis showed that in all instances no significant differences were found in ordination space between communal and private sites.

Vegetation type	Axis 1		Axis 2	
	mean	CV	mean	CV
HV private	-0.56	0.43	0.69	0.20
HV communal	-0.43	0.21	0.78	0.23
WK private	-0.18	0.08	0.59	0.23
WK communal	-0.13	0.10	0.56	0.24
MS private	-0.37	0.16	-0.57	0.67
MS communal	-0.57	0.48	-0.15	0.36
RV private	0.04	0.26	-1.61	0.42
RV communal	0.07	0.12	-1.67	0.60
EK private	0.48	0.37	0.01	0.16
EK communal	0.46	0.23	0.06	0.15
BE private	0.50	0.26	0.52	0.24
BE communal	0.22	0.12	0.38	0.16

4.3.3 Species richness and growth form composition

A total of 619 species was recorded in the study. Although there were no significant differences overall in the number of species recorded in the communal area and privately-owned farms for both lowland and upland habitats (Table 4.4), there were

significantly more species on the communal area at the 10 m^2 sample area (Figure 4.2). No significant difference was measured for any sample area for the upland habitats (Figure 4.3).

On the lowlands a significant shift in compositional cover was evident with reduced woody and succulent shrub cover and increased dwarf perennial cover on the communal area (Table 4.4). On the upland areas no similar compositional shift was recorded. However, perennial grass cover was significantly greater for rangelands on privately-owned farms (Table 4.4).

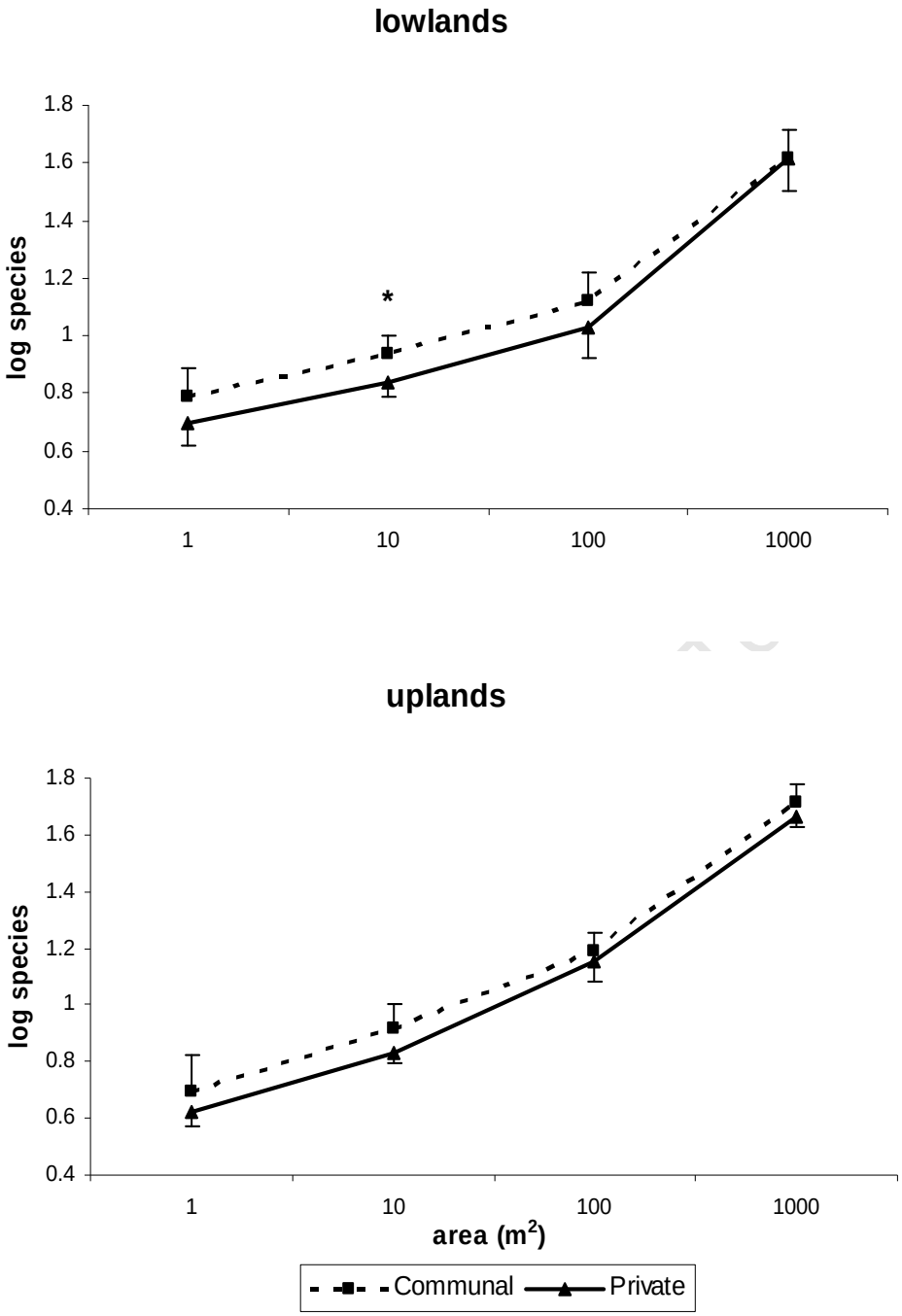


Figure 4.2 Log of mean species number by area (±SD) for all lowland (n = 36) and all upland (n = 30) sites for all vegetation types sampled in the study. Species numbers differ significantly at the $10m^2$ area on the lowlands only and this is indicated by an asterisk (*) ($F = 8.05$; $p = 0.008$).

Table 4.4 The mean (±SD) percentage cover per plot contributed by each growth form, and mean total cover and species number in 66, 0.1 ha modified Whittaker plots in lowland and upland vegetation across a fence separating communal areas from privately-owned farms in the Kamiesberg. The significance of across-fence differences were tested using a Wilcoxon matched pairs test; z scores and significance levels are given. Growth form definitions are given in 4.2.1.

Growth form	Lowlands				Uplands			
	Communal	Private	z score	p (n = 30)	Communal	Private	z score	p (n = 36)
Annual herbs	3.7 ± 2.9	3.3 ± 2.0	0.68	NS	1.7 ±1.4	2.2 ± 1.7	1.20	NS
Annual grass	0.2 ± 0.3	0.2 ± 0.4	0.84	NS	0.4 ± 0.6	0.2 ± 0.3	0.37	NS
Geophytes	0.5 ± 0.4	0.3 ± 0.3	1.59	NS	0.2 ± 0.3	0.5 ± 0.8	0.41	NS
Perennial grass	4.0 ± 8.4	5.1 ± 9.5	1.60	NS	1.0 ± 1.6	1.8 ± 2.9	2.34	0.02
Dwarf shrubs	4.4 ± 3.6	2.3 ± 2.0	2.27	0.02	2.5 ± 3.2	2.8 ± 3.3	0.28	NS
Woody shrubs	10.3 ±10.1	16.0 ± 15.3	2.59	0.01	18.4 ± 11.7	22.3 ± 13.9	0.94	NS
Succulents	10.0 ± 10.1	17.7 ± 15.3	1.98	0.05	8.6 ± 10.1	8.5 ± 8.7	0.37	NS
Trees	0.3 ± 0.9	0.0 ± 0.0	1.35	NS	0.6 ± 0.9	2.2 ± 4.5	0.52	NS
Total cover	33.2 ± 10.1	44.5 ± 11.1	3.12	0.0017	34.2 ± 14.4	42.0 ± 15.4	2.29	0.02
Total species	42.5 ± 11.7	42.5 ± 13.3	0.21	NS	49.8 ± 9.2	46.2 ± 7.6	1.29	NS

4.4 DISCUSSION

Because there were no significant differences in abiotic factors across the fence for both lowland and upland sites it is assumed that any differences measured in this study are in response to the significantly different grazing histories of the communal areas and privately-owned farms. Despite a long history of relatively heavy grazing pressure across the Leliefontein communal area, the six vegetation types surveyed in this study have not become homogeneous in response to this land use pressure. Each vegetation type appears to have retained its characteristic composition. The convergence, or homogenisation of vegetation types in terms of composition and cover in response to grazing pressure is reported internationally (James et al., 1999), in other semi-arid areas of South Africa (Hoffman and Cowling, 1990, 1991; Rutherford et al., 1995), and in localised studies in Namaqualand (Todd and Hoffman, 1999; Riginos and Hoffman, 2003; Petersen et al., 2004). However, at this scale, across the Kamiesberg, the vegetation has retained its high beta diversity, described as typical of the Succulent Karoo biome (Cowling et al., 1999a). All six vegetation types are situated on the relatively uniform granite-derived soils of the region (Watkeys, 1999), and are differentiated by the gradient presented by the Kamiesberg mountain, where climate and altitude, and as presented in Chapter 3, an array of soil variables, account for high turnover in species and vegetation types (see Chapter 3). Despite the generally lower grazing impact on upland sites, considerable overlap in species composition occurs between these two habitats and no obvious land-use composition pattern was detected.

However, an examination of the change in growth form composition, as suggested by the findings of Todd and Hoffman (1999) does show a land use response. There is a dramatic loss in overall plant cover on the communal areas. On the lowlands this loss is not spread evenly among all plant species, but a pattern emerges of variable distribution between different growth forms. Despite their apparent high variability in compositional cover, a uniform response in the loss of large succulent and woody shrubs and an associated increase in smaller dwarf shrubs and more ephemeral herbs, is evident across the lowland areas of all the vegetation types sampled. Here intense selective grazing pressure reduces the populations of large woody shrubs and

succulent shrubs such as *Lebeckia sericea*, *Zygophyllum retrofractum, Wiborgia monoptera*, and *Aridaria brevicarpa*. As these populations decline through reduced recruitment as flowers are grazed and eventually older shrubs die off, there is more available open space and a release in competitive pressure (Todd and Hoffman, 1999). There is a simultaneous selection for low, prostrate growth forms, which is recorded in similar studies and described as an avoidance mechanism (Milchunas et al., 1989). This is evident in this study in the proliferation of species such as *Limeum africanum* subsp. *africanum*, *Lessertia diffusa*, and *Lotononis pentaphylla.* This shift in compositional architecture in response to grazing is reported elsewhere in the literature for similar semi-arid areas. In Israel for example Hadar et al. (1999) report an increase in 'smaller species', while in Australia Fensham et al. (1999) report an increase in ground-hugging, trailing legumes in response to grazing around water points, where these highly palatable species, which avoid consumption by lying close to the ground, respond to the competitive release as tall perennial grass is grazed out (Fensham et al., 1999; Hadar et al., 1999). Grazing pressure also results in the selection of more ephemeral, typical r-selected species which are characteristically smaller, shorter-lived, and have a higher and earlier reproductive response, giving them a competitive advantage in colonising open space (Grime, 2001). In this study this would be the case for herbaceous perennial species such as *Ballota africana*, *Othonna oleracea,* and *Hypertelis salsoloides* var. *salsoloides*.

The failure to record an increase in annual cover, where Todd and Hoffman (1999) recorded significant increases in cover in these growth form classes for one of the vegetation types sampled in this study, is attributed to variable rainfall. In the year of their study, rainfall at Springbok, about 80 km north of the study area, which normally receives 200 mm per annum was 375.5 mm, while in 2002, the year of sampling for our study, rainfall was 145.5 mm. The mechanism that would give rise to a system of large patches dominated by annual herbs and geophytes in response to a pulse of rainfall, namely the reduction in cover of large perennial shrubs, is recorded in this study (Chesson et al., 2004). Given this, it is assumed that in a better rainfall year, similar increases in annual and geophyte cover would have been recorded.

The upland habitats on the communal area also experience a significant loss in cover. However, there are reductions in all compositional groups, with the only significant

shift recorded in the reduction of perennial grass on the uplands of the communal area. This suggests that the upland areas are buffered against grazing, as suggested by previous studies, where the accessible lowland areas are more readily grazed than the rocky uplands (Cowling et al., 1994; Todd and Hoffman, 1999; Riginos and Hoffman, 2003; Petersen et al., 2004; Pienaar et al., 2004). However, the evident loss of perennial grass on the upland areas of the communal area is possibly an early warning that these areas are now experiencing greater pressure, where the high palatability of grass means it may be the first compositional group to show a grazing response. This is supported by recent work in the Bushmanland ecotone which has shown the grasses in this area as competitively vigorous, suggesting in this instance that the perennial grasses are being targeted, where homogenous grazing would potentially favour an expansion of grass cover (Shiponeni, 2007). Grass cover on the uplands cannot be attributed to any one grass species, but is rather from a number of different species, including *Ehrharta calycina*, *Chaetobromus dregeanus*, and *Ehrharta barbinodis*. The high grass cover recorded on the lowlands is largely due to the dominance of *Stipagrostis brevifolia* in the Bushmanland ecotone. The lack of an equivalent response in grass cover in response to heavy grazing on the lowlands is attributable to two factors. Firstly, the high degree of grazing on the lowlands, while apparently higher on the communal lowlands, may have has resulted in a homogenisation in perennial grass cover on both sides of the fence. Secondly, there is a greater tendency for private farmers to keep cattle in addition to small stock, while communal farmers tend to keep only sheep and goats. Therefore, the presence of these bulk grass-grazers on the private farms serves to reduce the grass cover on the private farms, masking the variable stocking rate impact across the fence. This hypothesis of a current change in plant species composition would counter the suggestion that the state of the communal rangeland has not changed in the last 45 years (Benjaminsen et al., 2006), and warrants further investigation.

The Succulent Karoo is renowned for its plant richness and species richness data for this study is within the range of previous studies (Cowling et al., 1989; Milton et al., 1997). While species richness is not impacted by grazing at the 0.1 ha level, at the smaller sampling scale, and significantly so at the $10m^2$ area on the lowlands, species richness is higher on the communal area. This supports the findings of the compositional shift, where at a fine scale, more individuals can fit into a small area on

the communal lands with the loss of larger plants and the proliferation of smaller plants, and this in turn results in a higher measure of species richness (Oksanen, 1996). Again, in a higher than average rainfall year, this pattern is likely to be stronger, when open space is colonised by geophyte and annual species in a pulse response to high seasonal rainfall (Chesson et al., 2004).

Both the dramatic reduction in plant cover and the compositional shift, where the rangeland increasingly comprises smaller, more ephemeral species, recorded on the communal area, is cause for concern in an area where people are partly dependent on natural resources for their livelihoods. The current state of this range suggests that forage production is more strongly tied to rainfall than in a rangeland which is dominated by a higher proportion and cover of perennial shrubs (Todd and Hoffman, 2000). In good rainfall years an increased abundance in annual cover may be beneficial, albeit short-lived. In average to poor rainfall years or years where the rainfall is late, however, there would be considerably less available forage on the communal area (Chesson et al., 2004). Differences across the fence in terms of forage production and availability would be highlighted with considerable cost to those dependent on the range for their livelihood (Dube and Pickup, 2001). Climate variability is recognised as one of the most pervasive stresses to rural communities (Scoones, 1997; Ziervogel and Calder, 2003; Hesse and Cotula, 2006), and given the current trends documented in this study, this variability in forage production is likely to be exacerbated by predicted climate change for the Succulent Karoo (Rutherford et al., 2000; Hulme et al., 2001; Midgley et al., 2001).

This study shows that species richness is not affected by sustained heavy grazing except at a fine scale. However, species richness is determined by seasonal, annual, and spatial variation in rainfall, and only limited confidence can be attributed to a once-off assessment, particularly in a system described as slow to change (Wiegand and Milton, 1996). Cowling et al. (1994) caution that functional redundancy, suggested as characteristic of the diverse Succulent Karoo biome, need not imply resilience to loss of biotic diversity. They warn that the loss of species generally, be it to grazing or predicted future climate change, will reduce the capacity of these plant communities to respond to environmental fluctuation.

This study shows that despite sustained heavy grazing, each vegetation type in the study remains characteristically different, dominated by its own suite of species. No one species dominates the heavily grazed rangelands of Namaqualand. This high compositional turnover across the study area is consistent with our understanding of diversity in the region. While species richness is not impacted by grazing at the 0.1 ha scale, plant cover is significantly negatively impacted through sustained heavy grazing on both the lowland, and more unexpectedly, the upland habitats of the communal area of the Leliefontein reserve. This change in cover is variably evident in different growth form responses. On the lowlands these shifts are in keeping with other international studies and previous work in the area, with a uniform loss in large shrub cover and an increase in cover of smaller species. This compositional shift is also evident in the species area curves, where at the finer sampling scale, the communal area has a greater number of species. On the uplands the loss in cover is chiefly shared between all compositional groups, with evidence of a selective shift in a loss in perennial grass cover on the communal area. This points to a system where upland habitats are somewhat buffered against the effects of heavy grazing, but the shift in the highly palatable element suggests these upland habitats have also experienced some density-dependent grazing impact. With government plans to redress landownership issues in Namaqualand, with an expansion of the communal areas, consideration needs to be given to the implications of continued heavy grazing for the sustainability of people's livelihoods in the area.

5. DOES A PLANT FUNCTIONAL TYPE APPROACH PROVIDE ADDITIONAL INSIGHT INTO THE IMPACTS OF SUSTAINED GRAZING ON THE VEGETATION OF THE KAMIESBERG?

Abstract: In this chapter potential grazing impacts associated with the sustained heavy grazing of the communal rangeland are explored through a plant functional type approach. An informative typology is derived for the area that does show some grazing responses. The results support earlier findings in this thesis, and elsewhere, of a loss of longer lived woody perennials in favour of faster growing annual and herbaceous plants. An examination of plant functional type within growth forms as suggested in the literature does not provide any additional insights, whereas looking at traits alone does show some limited grazing response. There is also some evidence of a biogeographic shift, with an increase in a succulent-dominated plant functional type at the higher altitudes on the communal rangeland. However, the findings of this analysis are not as strong or as clear as either previous findings in this study, or as anticipated. This is attributed to the fact that too broad a brush was used in adopting the proposed universal language advocated by plant functional type practitioners in an attempt for easier global comparisons. For example growth form height classes are too coarse for the shorter vegetation of the Succulent Karoo. In the resultant 'fuzzy' groups, some responses are lost. On this basis there is limited scope for the development of indicator types. While this method is informative and thought provoking, in eliciting grazing responses there is a stronger case for the more simple growth form analysis adopted in Chapter 4.

5.1 INTRODUCTION

The high degree of diversity among plant species has always captivated botanists. However, it is this same variation that can in turn limit the scale of studies, often making them only locally relevant (Rutherford et al., 1995). This has led ecologists to look for a 'common currency' by simplifying this diversity through categorising plants on the basis of physiological and morphological affinities (Rutherford et al., 1995; Landsberg et al., 1999). This is broadly termed a plant functional type approach.

The general principles of a plant functional type approach are by no means new to ecology and several authors recall Theophrastos' *Historia Plantarum*, dated to around 300 BC, which gives the first recorded morphologically-based classification (Gitay and Noble, 1997; Diaz Barradas et al., 1999; Weiher et al., 1999). While the essential

elements of Theophrastos' basic growth-form classification persist, classifications have become more and more refined. The last two decades in particular have seen a proliferation of work in the area of plant functional types. This is largely in response to pressing questions around the impacts of land use and climate change, where ecologists are searching for universal response patterns (Lavorel et al., 1997). Plant functional types have been derived in a number of different ways and for a number of different purposes (McIntyre and Lavorel, 2001). Definitions of what constitutes a plant functional type are equally numerous, and linked to the nuances of each particular study. Lavorel et al., (1997), however, provide a useful general definition and suggest that plant functional types are non-phylogenetic categories of species grouped according to shared morphological and physiological traits. With respect to disturbance studies, this is based on the idea that a disturbance such as grazing is not random, but depends on and affects certain plant traits more than others, and response patterns emerge where species selected through the disturbance pressure share some converging traits (Stafford Smith and Pickup, 1993; Louault et al., 2005; Diaz et al., 2007). The functional aspect is linked to the tight relationship between form and function (Shugart, 1999). On this basis, species grouped according to plant functional type characteristics, where they are assumed to share similar resource-use patterns and ecosystem roles, should respond similarly to environmental conditions or disturbance (McIntyre et al., 1999b; Navarro et al., 2006). It is easy to see that should such patterns emerge, plant functional types could make extremely useful management tools where indicator types could be generated and predictive models developed.

Furthermore, a plant functional type approach allows for regional comparisons with the formation of a common language through which taxonomically distinct and complex systems can be effectively compared (Rutherford et al., 1995; Landsberg et al., 1999). On this basis it is recommended over a floristic approach, where plants are grouped according to phylogenetic relationships, in its ability to simplify the complexity of taxonomically diverse areas and thereby aiding global comparisons (Diaz et al., 1999; Sala et al., 1999). It is an informative approach, described as operational or mechanistic, where the classification itself gives insight into how and why species respond the way

they do, and in turn the functioning of the ecosystem (Gitay and Noble, 1997; Skarpe, 1997; Diaz et al., 1999; Landsberg et al., 1999). Skarpe (1997) describes plant functional types as the 'acting and reacting units' which respond to changes in environmental conditions. This is particularly significant in disturbance studies, where the convergence of characteristics may signal a common response and can improve assessments of ecosystem sensitivity to change (Diaz et al., 1999; McIntyre et al., 1999b). This search for common trends in response to disturbance allows for generic predictions and potentially more proactive management where the successful development of plant functional types means response types can be developed for monitoring purposes (Diaz Barradas et al., 1999; Landsberg et al., 1999). Linked to this is the increasing recognition that dominant plant traits in turn affect ecosystem function, and on this basis plant functional type studies can readily feed into ecosystem service studies or plant community modelling exercises (Diaz et al., 1999). McIntyre et al. (1999a) describe plant functional types as effective ecological frameworks for exploring vegetation response (McIntyre et al., 1999a) and indeed the approach has been widely adopted in the formation of predictive models. Several authors propose a collection of traits that form a syndrome and that these in turn can be seen as strategies, which essentially make up a functional type (Landsberg et al., 1999; Reich et al., 2003). These strategies are evident in a number of models (Diaz et al., 2007), for example such as Grime's (Grime, 2001) Competitive-Stressor-Ruderal (C-S-R) response model, and more specifically related to grazing, Noy-Meir et al.'s (1989) 'increaser', 'decreaser' and 'neutral' species grazing response model. The variety of models and the number of different approaches to plant functional type studies show the persistent desire to reduce the complexity of nature into accessible response units to allow for prediction. Clearly, the development and use of a common language such as proposed by the plant functional type approach would allow for a much greater depth of data exploitation (Weiher et al., 1999).

With so much emphasis on the value of a plant functional type approach as a useful ecological tool, it begs the question as to how successful this method of analysis has been in bringing to light common grazing responses. From the vast number of studies exploring grazing impacts through plant functional types some consistent findings,

predominantly of life history and gross morphological and structural traits, do emerge. Most universal is that heavy grazing favours annual species, or herbaceous forbs described as 'facultative annuals', over perennial species (Kleyer, 1999; Todd and Hoffman, 1999; Diaz et al., 2007) (see also Chapter 4). In terms of growth form and structure, grazing favours small-statured and prostrate species over taller and more erect species (Tilman, 1982; Noy-Meir et al., 1989; Fernandez et al., 1993; Friedel et al., 1993; Hadar et al., 1999; Landsberg et al., 1999; Lavorel et al., 1999; Grime, 2001; Diaz et al., 2007)and those with rosette, and stoloniferous growth forms, over tussock growth forms (Lavorel et al., 1998; Lavorel et al., 1999). A number of other less frequently recorded responses exist relating, for example, to seed size, dispersal mode, spinescence, and palatability (Lavorel et al., 1997; Landsberg et al., 1999; Westoby and Leishman, 1999; McIntyre and Lavorel, 2001; Diaz et al., 2007). It is also important to note that some studies have not found strong plant functional type responses, even in cases where responses were anticipated (Fernandez et al., 1993; Friedel et al., 1993; McIntyre et al., 1999b; Cousins and Lindborg, 2004).

While common responses do exist, these are only a handful and the quest for universal response patterns through plant functional types has proved somewhat frustrating. Aside from the gross morphological and life history findings listed above, no other universal patterns emerge, and even these largely common responses appear in varying degrees (Landsberg et al., 1999). As shared global patterns are sought the importance of land use and grazing history in combination with regional climate in determining plant functional type responses is increasingly noted (Reich et al., 2003; Diaz et al., 2007). In their exhaustive synthesis of plant functional type responses to grazing, Diaz et al. (2007) demonstrate that the search for common responses is more subtle, and that common responses are frequently constrained to regions of similar climate and evolutionary and land-use history (Diaz et al., 2007). A further suggestion in the quest for universal response patterns is to search for plant functional types within the macro-scale growth forms, where perhaps side stepping these more obvious traits may give insight to a more universal grazing response across the growth forms which may be currently obscured by them (Lavorel et al., 1997; Landsberg et al., 1999; McIntyre et al., 1999b, 1999a). While

widely advocated as a useful approach, in taking stock of a vast number of previous studies, researchers suggest a more refined approach, where common responses be sought in climatically and historically similar regions, and a more considered approach to the actual analysis be adopted.

This chapter examines the impacts of the sustained heavy grazing associated with the communal rangelands of the Kamiesberg using a plant functional type approach. In doing so it questions the validity of adopting a plant functional type analysis in expanding our understanding of plant community response to grazing. More specifically, this chapter sets out to address the following questions:

1. What is the plant functional typology for the area?
2. Using Noy-Meir et al.'s (1989) 'increaser', 'decreaser', and 'neutral' model, how is each emergent functional type likely to respond to the sustained grazing on the communal range?
3. How does each emergent functional type respond to the sustained heavy grazing on the communal range, and how is this affected by altitude and the variable upland and lowland habitats?
4. Does considering plant functional types within growth forms, as suggested by previous authors, give a more meaningful insight into grazing responses?
5. Does a look at traits alone provide any additional insights?
6. What is the potential for developing indicator types?

5.2 METHODS

5.2.1 Data collection

Species lists and plant cover values collected in the 66 Whittaker plots across the full range of the Kamiesberg were used in this analysis (see Chapter 4). Also used in this study are the grazing scores previously generated in the same data collection process. For each species, traits were collected from field measures, herbarium specimens, floras for the region, for example LeRoux (2005), and botanical experts working in the same

geographic area. Traits fall into life history, morphology and regeneration categories. Traits were selected on the basis of relevance to grazing and colonisation response. Definitions for each category were based primarily on the work of Corelissen et al. (2003) who have developed a handbook of protocols in an attempt at standardising plant functional type studies. However, when the number of species for a category was less than 20, category definitions were broadened to allow for integration. Size divisions within some categories were based on histograms (e.g. leaf size). Some additional categories (e.g. flower number), were included as these were viewed as valuable in terms of examining grazing responses. Where a category had no plants it was excluded. Twelve categories and subcategories of traits were defined, giving a total of 33 traits (Table 5.1). In a few cases data were unavailable (e.g. for palatability). In these instances rather than reduce the species list, especially where an otherwise full complement of traits was recorded, a middle value was allocated to the species. While all original measures were taken in recommended units, a binary matrix of traits was ultimately established for the 619 recorded species.

Table 5.1 Traits and subgroups within traits, and defining characters for each, used in this plant functional type analysis. Traits and defining characteristics are based on Corelissen et al. (2003). Those additional traits included are marked by an asterisk. In instances where smaller trait groups were merged, the name of the more dominant trait has been kept.

Traits	Subgroup	Description / defining terms
Growth Form	Short basal	Leaves < 0.5 m long, prostrate
	Long basal	Leaves > 0.5 m long, prostrate, not tussock forming
	Erect leafy	Plant erect with leaves concentrated near middle and top. Merged with 'semi-basal', to include those with leaves at the base and middle. Also merged here are 'palmoids', those with rosette leaves at the top of a stem and 'epiphytes', all those plants growing in others.
	Tussock	Many leaves from basal meristem forming prominent tufts. Merged with 'cushions', to include tightly packed foliage held close to the soil surface.
	Dwarf shrub	Woody plants up to 0.8 m tall.
	Shrub	Woody plants taller than 0.8 m with canopy deployed relatively close to the soil surface. Merged with 'trees', to include elevated canopies. Also merged with 'leafless shrubs or trees' with green, non-succulent, photosynthetic stems.
	Leaf succulents	Includes all leaf succulents through the merging of categories 'short leaf succulents' and 'tall leaf succulents'.
	Stem succulents	Includes all stem succulents through the merging of categories 'short stem succulents' and 'tall stem succulents'.
*Longevity	Perennial	Lives longer than one year.
	Annual	Life cycle complete within one year.
*Geophyte		Those perennial herbaceous plants with underground storage organs. The area has many geophytes warranting a separate classification.
Plant height		The shortest distance between the upper boundary of the main photosynthetic tissue on a plant and the ground level.
	Small	< 0.3 m
	Medium	0.31 – 1.0 m
	Large	> 1 m
Clonality		Those plants with the ability to reproduce vegetatively. Includes merged categories of above and below ground clonality.
Spinescence		Merged to include any form of spinescence, including spines, thorns or prickles.
*Palatability	Unpalatable	Never to rarely grazed
	Moderate	Occasionally grazed
	Very	Readily grazed
*Leaf type	Simple	Simple leaf
	Lobed	Any deviation from a simple leaf
Leaf longevity		Time period during which an individual leaf is alive.
	Deciduous	Leaves last only one season
	Semi-deciduous	Some leaf loss throughout the year and or leaf loss in response to drought
	Evergreen	Leaves persist all year round
Leaf size		One sided projected surface area of an average leaf
	Small	<100 mm^2
	Medium	101 - <500 mm^2
	Large	> 500 mm^2
*Flower number	Few	< 10 flowers per plant
	Moderate	Between 10 and 100 flowers per plant
	Lots	> 100 flowers per plant
Dispersal mode	Unassisted	Seed or fruit has no obvious aids for longer-distance dispersal, falls passively.
	Wind	Includes minute seeds, seeds with pappus, 'balloons', flattened seeds with 'wings' and 'tumbleweeds'
	Other	Includes all forms of animal dispersal, water dispersal (hydrochory and hygrochastic mechanisms)

5.2.2 Statistical analyses

A data-defined approach was adopted (Gitay and Noble, 1997; Skarpe, 1997) where multivariate techniques were used to cluster species into groups according to the chosen traits. The database was analysed using a hierarchical clustering method. The selection of traits was considered, and the nature of the grazing disturbance and measurability were influential, but no subjective weighting was used to avoid the formation of classifications dominated by preconceptions (Leishman and Westoby, 1992; Hobbs, 1999; Westoby and Leishman, 1999). PC-ORD was used for the cluster analysis and the euclidean distance measure and group average linking were used (McCune and Grace, 2002). On the basis of the hierachical cluster analysis, plant functional types were defined. These plant functional types were then examined to see which traits were associated with each group. The dominant traits, those present in more than 50% of the species comprising the plant functional type, were considered relevant to that group (Leishman and Westoby, 1992). The relative abundance of species with less common attributes, such as spinescence, were compared between the groups, and the plant functional type with the highest presence of that trait noted.

For each derived plant functional type a predictive model was produced, and each plant functional type attributed 'increaser', 'decreaser' or 'neutral' status according to Noy-Meir et al.'s model (1989). 'Decreasers' are those species whose relative abundance decreases consistently in response to heavy grazing, and 'increasers' inversely increase in abundance. 'Neutral' species show no response to grazing pressure (Noy-Meir et al., 1989).

The presence according to relative and absolute percentage cover for each of the plant functional types generated was established for each site. A paired Wilcoxon sign-rank test was used to test for significant differences in the six plant functional types according to plant cover and species number, on either side of the fence. Upland and lowland habitats were considered jointly and separately. For each plant functional type cover was correlated with the grazing score attributed to each site (see Chapter 4).

A separate analysis was carried out for each individual growth form following the procedure outlined above, where a hierarchical cluster analysis was used to generate groups within each basic growth form. Cover of the various plant functional types derived within the growth forms was then compared statistically, with consideration of communal and private land use and habitat type.

The species-by-traits matrix was multiplied by the species-cover-by-sites matrix. Using this matrix, the percentage contribution of each trait to each site was generated. These were then tested for significant differences with consideration as to land use and habitat type, using a single factor ANOVA. In those instances where data were not normal, the non-parametric Mann-Whitney U test was used.

To explore the grazing response of the plant functional types to different land use pressure across altitude, the relative cover of each plant functional type was correlated with altitude for communal and private rangelands. A test for homogeneity of slopes was then carried out to look for significant differences in slope in relative cover between the communal and private rangelands with altitude. All data were analysed using STATISTICA 7.

5.3 RESULTS

The hierarchical cluster analysis produced six clusters of nested subsets which were in turn interpreted as six plant functional types (Figure 5.1, Table 5.2). The emergent typology is largely dominated by growth form. Plant functional type 1 predominantly comprises smaller leaf and stem succulents. Plant functional types 2 and 3 are both shrub groupings; with plant functional type 2 comprising small stature shrubs and tussocks with some clonality, while plant functional type 3 comprising somewhat larger and more erect shrubs. Plant functional type 2 is moderately to highly palatable, semi-deciduous and has the greatest presence of plants with lobed leaves. Plant functional type 3 has lots of

flowers and wind-dispersed seeds. Plant functional type 4 comprising the larger shrubs, which are evergreen, predominantly unpalatable and is the group with the greatest degree of spinescence. Plant functional types 5 and 6 are both highly deciduous. Plant functional type 5 accounts for the vast majority of annual species, and includes elements of all the smaller or more forb-like growth forms. Plant functional type 6 includes all the geophytes. The predicted model of each likely response to grazing based on Noy-Meir et al.'s (1989) 'increaser', 'decreaser' and 'neutral' model is also presented in Table 5.2.

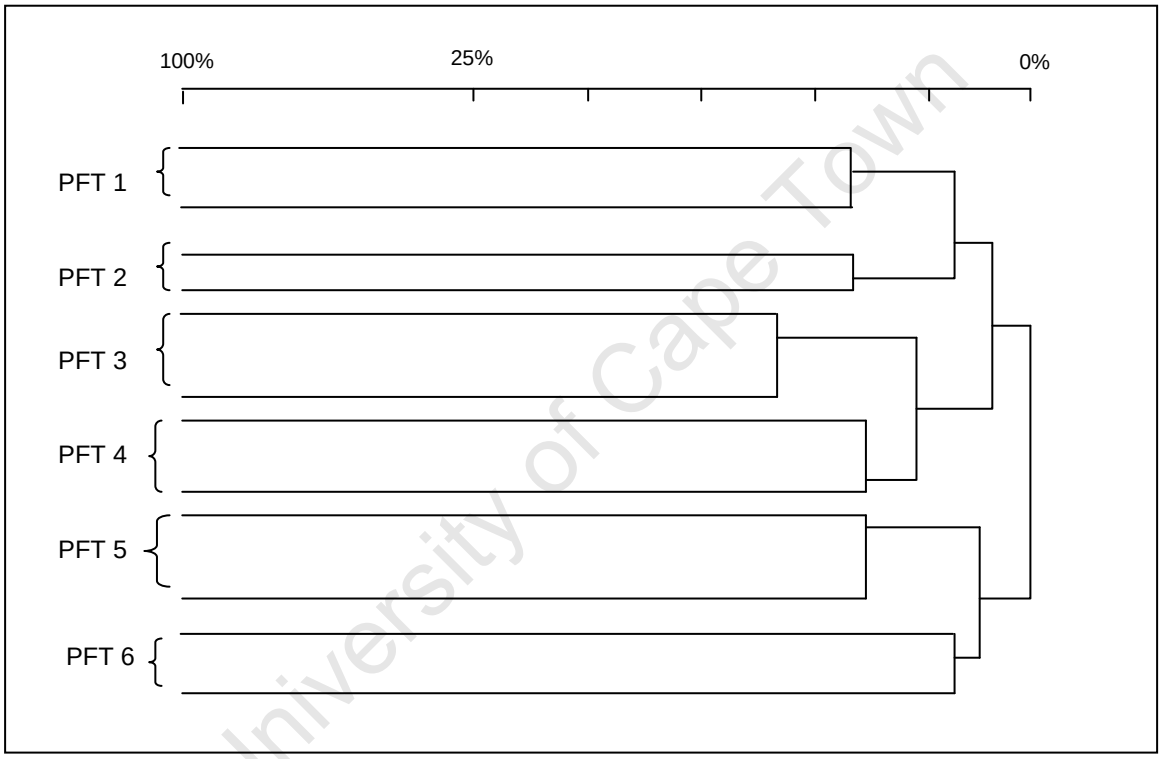


Figure 5.1 A schematic of the dendogram obtained on which the plant functional type groupings were generated. Note the scale of the 'percentage information remaining' bar at the top of the image changes for the purpose of clarity.

Table 5.2 Traits found in more than 50% of species in each plant functional type (PFT) group generated in the hierarchical cluster analysis. Where traits were never more than 50% in any grouping, those with the relatively highest measures are noted, such cases are indicated with an asterisk (*). Also included is the predicted 'neutral', 'decreaser', or 'increaser' response of each plant functional type.

Trait	PFT 1	PFT 2	PFT 3	PFT 4	PFT 5	PFT 6
Growth form	Dwarf shrubs Leaf succulents Stem succulents*	Dwarf shrubs Tussocks*	Shrubs Erect-leafy*	Shrubs	Erect-leafy* Tussocks*	Large-basal
Longevity	Perennial	Perennial	Perennial	Perennial	Annual	Perennial
Geophyte						Geophyte
Plant height	Small Medium*	Medium	Medium	Large	Small	Small
Clonality						Clonal
Spinescence				Spines*		
Palatability	Moderate	Moderate Highly*	Highly*	Unpalatable	Moderate	Moderate
Leaf type	Simple	Simple Lobed*	Simple	Simple	Simple	Simple
Leaf longevity	Evergreen	Semi-deciduous		Evergreen	Deciduous	Deciduous
Leaf size	Small*		Small			Large
Flower number	Moderate	Moderate	Lots	Lots	Moderate	Moderate
Dispersal mode	Other	Unassisted and wind	Wind	Unassisted	Unassisted	Unassisted and wind
Number of species	110	95	74	90	134	116
Predicted response to sustained grazing pressure	Neutral	Decreaser	Decreaser	Decreaser	Increaser	Increaser

For both relative and absolute cover for upland and lowland habitats combined, the only significant shift in response to the sustained heavy grazing on the communal side of the fence was in an increase in plant functional type 5 ($z = 2.18$, $p < 0.05$). Once separated on the basis of habitat, the only significant shifts were a decrease in plant functional type 2 on the lowlands ($z = 2.78$, $p < 0.01$) and an increase in plant functional type 5 on the uplands ($z = 1.98$, $p < 0.05$) (Figure 5.2). In terms of species numbers, with combined habitats, plant functional type 5 had significantly more species on the communal rangeland than on the private range ($z = 2.11$, $p < 0.05$) and once separated on the basis of habitat, this continued to be true of the upland habitats only ($z = 1.98$, $p < 0.05$) (Figure 5.3). Correlating plant functional type cover and grazing score, where a high grazing score reflects heavy grazing pressure, showed a negative correlation between plant functional type 4 and the higher grazing scores on the lowlands and a positive correlation between plant functional type 6 and the higher grazing scores on the uplands (Figure 5.4). While trends generated in these correlations reflect the findings of the pair-wise analysis for plant functional type 2 and 5, these are not significant.

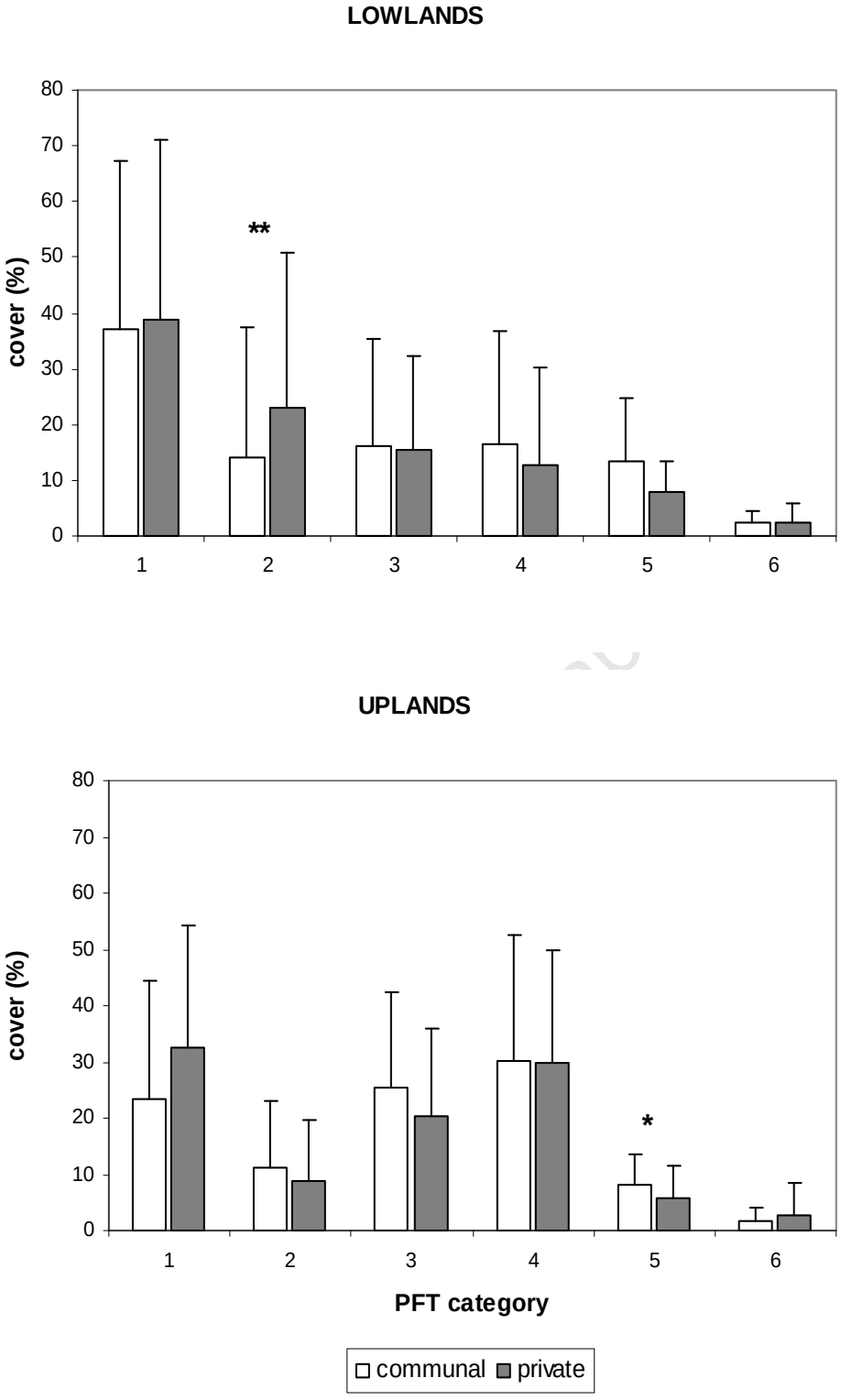


Figure 5.2 The mean (±SD) relative cover of each plant functional type on communal and adjacent privately owned rangeland. Asterisk (*) indicates significant differences between the two land uses at the $p < 0.01$ (*) and $p < 0.05$ (**) level respectively.

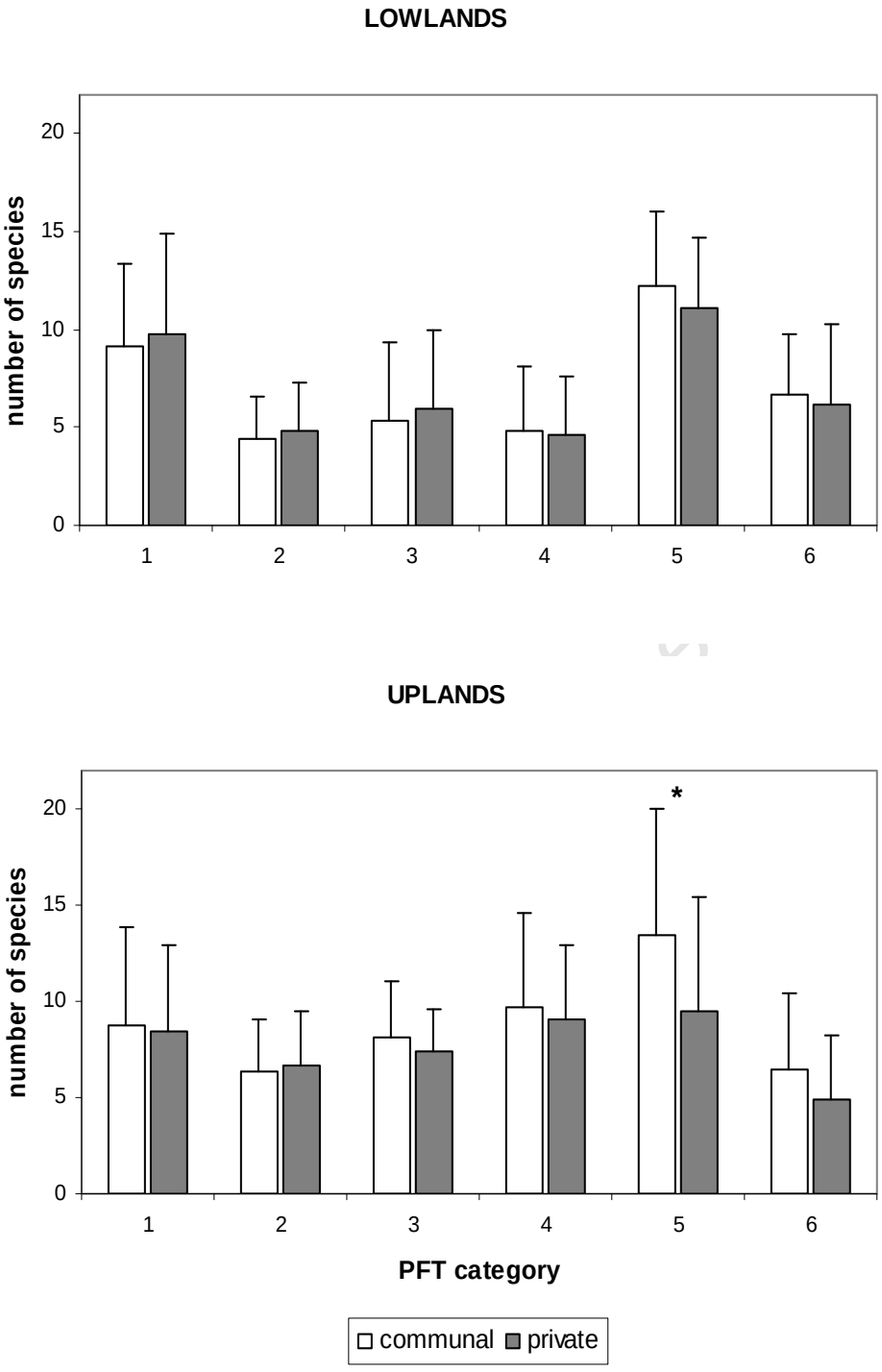


Figure 5.3 The mean (±SD) species number for each plant functional type on the communal and adjacent privately owned rangeland. Asterisk (*) indicates significant differences between the two land uses at the $p < 0.05$.

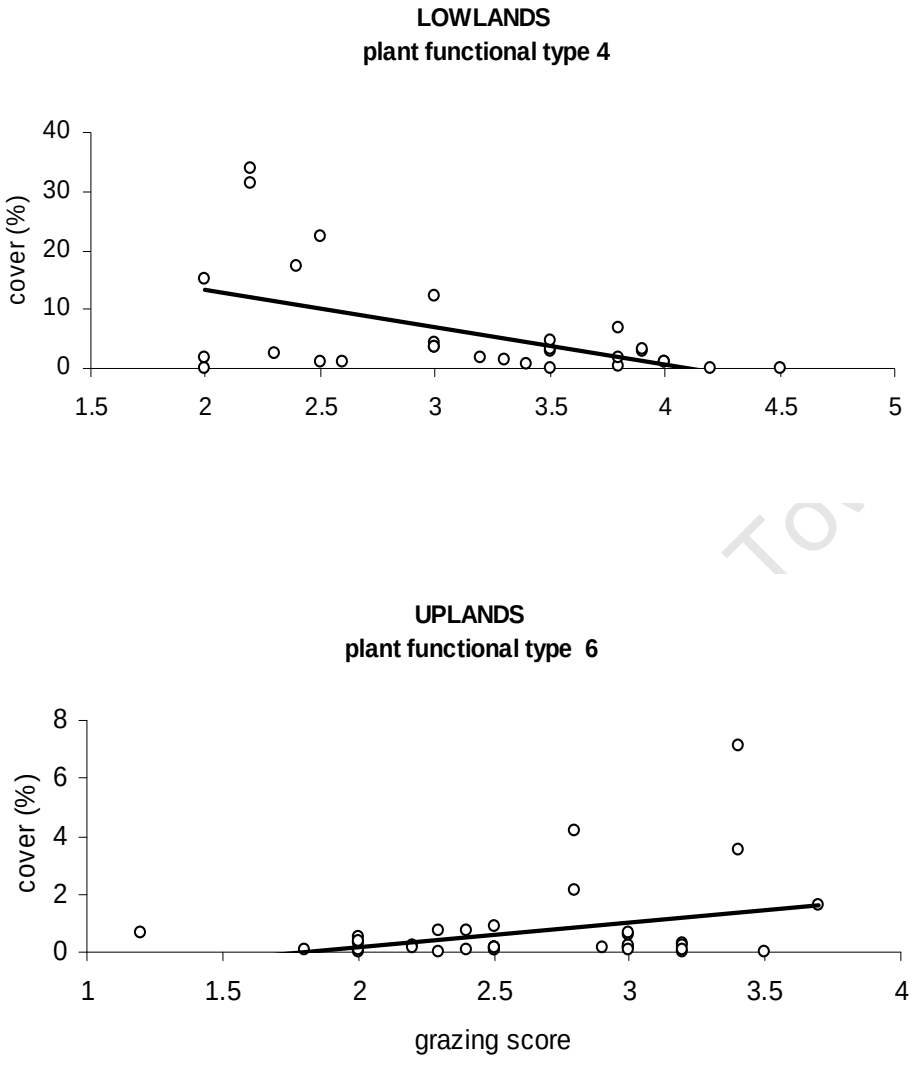


Figure 5.4 Significant correlations between relative cover of plant functional types 4 and 6 with the subjective grazing score (1 = low; 5 = high) for the lowlands and uplands respectively.

In exploring the value of plant functional types within each individual growth form, the cluster analyses generated between two and four groups in each individual growth form. There was no statistical variation in relative or total cover between any of these groupings within each growth form in response to the variable grazing pressure on communal and private rangelands.

The examination of traits showed a significant increase in the large basal and erect leafy growth forms in response to grazing ($F = 4.53$ and $F = 6.54$ respectively, $p < 0.05$). Medium height, simple leaves and few flowers all decreased in response to grazing ($F = 7.23$, $F = 4.37$, and $F = 4.87$ respectively, $p < 0.05$).

In correlating plant functional types with altitude, the only significant variation in slopes was found for plant functional type 1 (Figure 5.5). For the upland habitats there was a greater cover of plant functional type 1 with altitude than on the communal range ($F = 3.1$, $p < 0.05$). On the lowland habitats the inverse was true, where there was less cover of plant functional type 1 with altitude on the communal range ($F = 3.88$, $p < 0.05$).

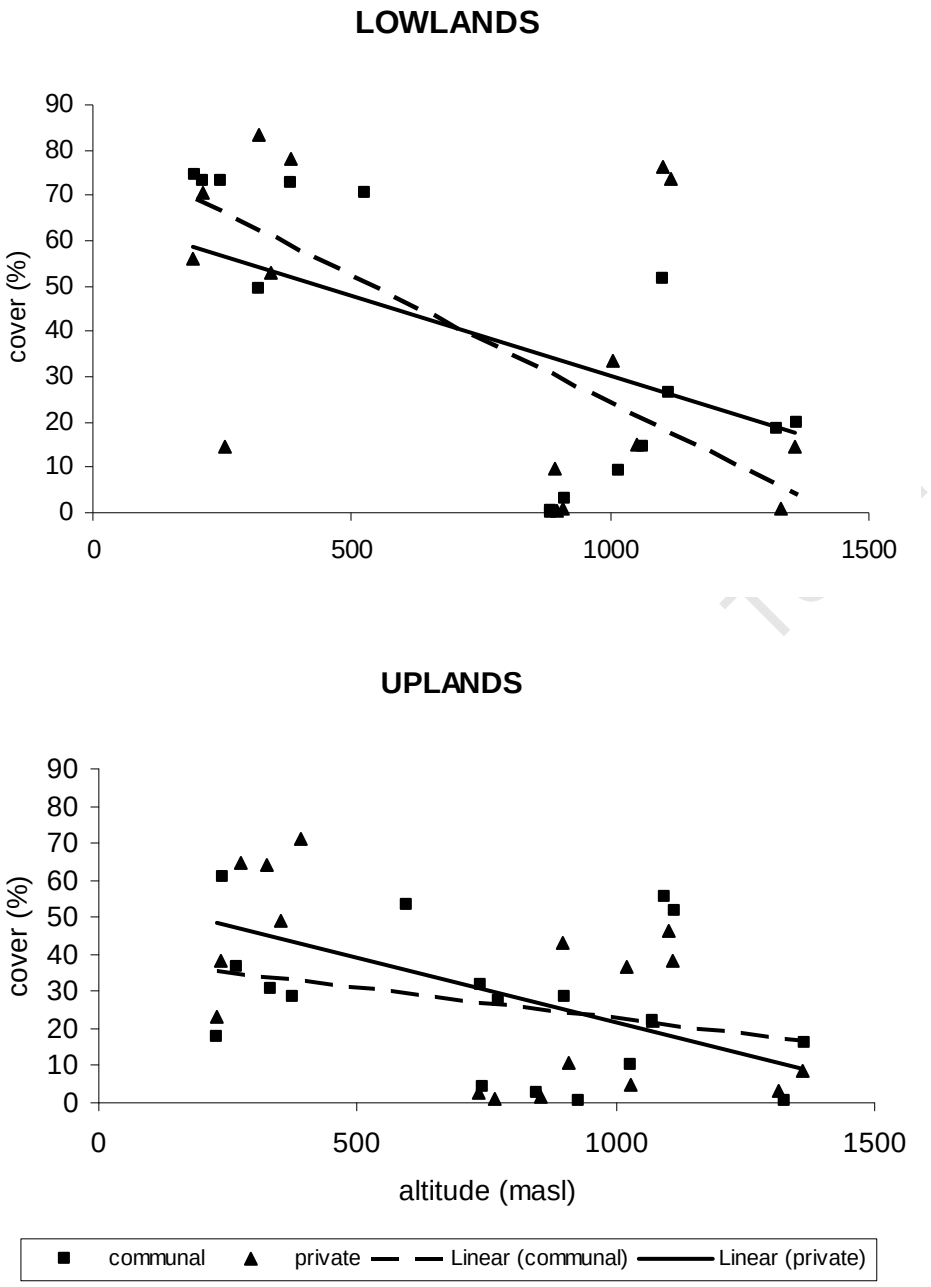


Figure 5.5 Correlations between relative cover of plant functional type 1 and altitude as found on the communal and private range respectively.

5.4 DISCUSSION

5.4.1 The plant functional typology for the area

The emergent typology for the area appears to be dominated largely by life history and growth form characteristics. On this basis some of the groups are clearly defined, such as plant functional types 5 and 6 which accounted primarily for the annual and herbaceous, and geophyte species respectively. While plant functional type 1 is succulent dominated, larger succulents were drawn into the larger shrub dominated functional types 3 and 4. Similarly, while plant functional type 2 chiefly comprises the shorter shrubs, plant functional type 3 does contain some short shrubs. This is the nature of hierarchical analysis, where similar entities may diverge on the basis of the fact that they merge with other entities, and can result in dilute groupings (McCune and Grace, 2002). This is in keeping with Kleyer's (1999) description of plant functional types as 'fuzzy' groupings of species (Kleyer, 1999). While grazing impacts are evident among some of these emergent plant functional types, these responses are less obvious than anticipated given the findings of the basic growth form analysis in Chapter 4. The value of the emergent typology and more generally the adopted approach is discussed following a closer examination of the findings.

5.4.2 Predicted and actual responses of plant functional types to grazing

The decrease in plant functional type 2 on the communal rangelands in the lowland habitat fits the prediction of this plant functional type as a grazing 'decreaser'. At first glance this may seem unlikely as one of the more common grazing disturbance responses, and indeed a response recorded in the analysis in Chapter 4, is an increase in dwarf shrubs, and plant functional type 2 is essentially dwarf-shrub dominated (Noy-Meir et al., 1989; Fernandez et al., 1993; Friedel et al., 1993; Hadar et al., 1999; Lavorel et al., 1999; Diaz et al., 2007). However, it is important to note that the qualification for dwarf shrub in this analysis is taken directly from that of Corelissen et al. (2003), in light of their plea for standardized protocols in the qualification of traits, and includes woody shrubs up to 0.8 m in height (Corelissen et al., 2003). In the growth form classes used in the grazing analysis in Chapter 4, dwarf shrubs are qualified as those shrubs less than 0.25 m in

height, and in that instance, qualifications were based on work by Cowling et al. (1994) who carried out similar work in the same geographic region (Cowling et al., 1994). This points to the difficulty in developing global models where similar terminology might be used for highly variable classes, or as in this instance where the flora may fall within a much narrower height spectrum and suggested qualifications could obscure responses. It is on this basis that I have resisted naming each of the plant functional type classes generated here, where terminology is not universally understood, and in some instances while dominated by a certain growth form, this is not exclusive to the plant functional type.

The significant reduction of plant functional type 2 on the lowlands in response to grazing is attributed to the frequently encountered loss of perennial woody shrubs in response to grazing disturbance (Ayyad and Elkadi, 1982; Noy-Meir et al., 1989; Olsvig-Whittaker et al., 1993; Todd and Hoffman, 1999) (see also Chapter 4). Plant functional type 2 also has the vast majority of lobed and compound-leaved perennials, which in this system are predominantly members of the Fabaceae, known for their nutritional value and palatability (El Mouden et al., 2006). The presence of these species, along with others, accounts for the moderate to high-palatability of this group. Plant functional type 2 also has a high number of semi-deciduous and some deciduous plants. Drought-deciduousness is typically selected for in arid systems (Chabot and Hicks, 1982), and some authors have described drought-deciduous grazing-tolerant functional types (Navarro et al., 2006). This is in contrast to this 'decreaser' group. This is ascribed to the fact that the output of leaves designed to maximise carbon gain only over those favourable times of the year means that these leaves are generally not as heavily defended as those of evergreen species where the carbon investment is higher, making deciduous or semi-deciduous leaves more appealing to grazers (Chabot and Hicks, 1982). Any loss of leaves through grazing will have a negative effect on a plant's carbon budget. Evidently in this study the type of leaves put out to maximise carbon gain over the short growing season are appealing to grazers and their loss is in turn expensive and debilitating.

Plant functional type 2 also contains the majority of the perennial tussock-forming plants, a reduction in which is in keeping both with previous studies, and the growth form analysis in Chapter 4 (Lavorel et al., 1998; Landsberg et al., 1999; Lavorel et al., 1999). These are mostly perennial grasses and their high palatability means they are often the first element to be grazed out of a rangeland. Plant functional type 2, a combination of medium shrubs and tall perennial grasses is a typical grazing 'decreaser', fitting the predicted model (Noy-Meir et al., 1989).

The increase in plant functional type 5 on the uplands fits the predicted 'increaser' model where annual species proliferate under heavy grazing, filling the gaps generated through the loss of perennial cover (Kleyer, 1999; Todd and Hoffman, 1999; Diaz et al., 2007; Lehsten and Kleyer, 2007) (see also Chapter 4). These are Grimes ruderals (1979) and Noy-Meir et al.'s (1989) 'increaser' species. It is important to note that plant functional type 5 includes a number of herbaceous forbs, or what might be termed 'facultative annuals'. The inclusion of these herbaceous forbs accounts for the expression of a grazing response here, where one is absent in the growth form analysis in Chapter 4. In Chapter 4 the annual category contained only annuals, and the herbaceous forbs in that analysis were included in the dwarf shrub category, which in turn showed a grazing response. Once again this highlights the importance of differences in approach, and justifies the reluctance to name the plant functional type groupings according to their dominant growth form when they are in fact 'fuzzy' groups comprises numerous elements. The fact that this increase in plant functional type 5 is only evident on the uplands shows firstly that the uplands do show a grazing response, but that this is no longer evident on the equivalent lowland habitats, which we know are more heavily grazed (Petersen et al., 2004; Samuels et al., 2007) (see also Chapter 4). It must once again be noted that the rainfall in the year of data collection was particularly low and this meant there were generally fewer annuals than anticipated. In a rangeland already under grazing pressure those few annuals that would come up in a dry year on the accessible and heavily grazed lowlands would almost certainly be the first elements to be grazed out. Once again we see that the grazing disturbance on the communal range selects for these more ephemeral elements with limited production and carbon storage. The system

is being steered towards one where nutrients are lost and plant community is increasingly vulnerable to environmental perturbation (Diaz and Cabido, 2001; Gondard et al., 2003).

While their were few significant differences in plant functional type cover between communal and privately owned farms, plant functional types 4 and 6 both showed a correlation with the grazing score generated at each site. The fact that these results only emerge in relation to the assigned grazing score is attributed to the fact that while attempts were made to avoid obvious confounding factors in the landscape such as stock posts or water points, some heterogeneity in localised grazing pressure may have been encountered. The fact that the responses of plant functional types 2 and 5 are lost in this analysis is likely to be due to the fact that the pair-wise analysis is more refined. Skarpe (1997) talks about the importance of scale and resolution in examining plant functional type responses to grazing. In the pair-wise analysis, sites are being compared within vegetation types giving better clarity by allowing for the nuances of abiotic considerations and environmental stresses and variability in dominant plant community structural elements encountered in the different vegetation types as outlined in Chapter 3. Plants frequently show a degree of plasticity and will respond variably to disturbance in different areas in light of these abiotic and biotic constraints (Milton, 1990b). It is possible that a pair-wise test allows for this between vegetation type variation, but in lumping all the functional types across the variable vegetation types for the grazing score correlation, a number of these more subtle variations are lost.

The positive correlation between cover of plant functional type 6, the group dominated by geophytes, and the higher subjective grazing scores shows the value of clonality in response to grazing. Clonality is described as giving plants considerable competitive vigour, tiding them through persistent droughts, and in particular in allowing them to exploit open spaces (Cowling et al., 1994; Weiher et al., 1999; Lehsten and Kleyer, 2007). The deciduous nature of geophytes adds to this, where the output of large leaves, closely correlated with high relative growth rates and in turn strong competitive ability, allows them to maximise their carbon gain through the short growing season without having to invest in persistent structures (Landsberg et al., 1999; Weiher et al., 1999;

Lehsten and Kleyer, 2007). The proliferation of plant functional type 6 dominated as it is by geophytes is a predicted and previously recorded, grazing disturbance 'increaser' response (Noy-Meir and Oron, 2001).

The loss of large woody perennial shrubs, such as those that dominate plant functional type 4, is a commonly recorded grazing response (Ayyad and Elkadi, 1982; Noy-Meir et al., 1989; Olsvig-Whittaker et al., 1993; Steinschen et al., 1996; Todd and Hoffman, 1999; Navarro et al., 2006). This response is one already recorded in this study (see Chapter 4), and in keeping with predictions of its 'decreaser' status made here. These slower to mature large woody shrub species, with evergreen leaves which are more expensive to produce and therefore more devastating to lose, renders these species vulnerable to intense grazing pressure (Chabot and Hicks, 1982; Reich et al., 2003). Plant functional type 4 also has a high degree of autochorous or unassisted seed dispersal, a suggested adaptation to arid areas, where the most favourable site is often the parent site (van der Pijl, 1982; van Rooyen et al., 1990). Indeed, autochory was common in this study accounting for 51% of the dispersal mechanisms. However, this limits the potential to occupy open spaces at a distance from the parent plant, making this group a poor post grazing coloniser. Plant functional type 4 also has the highest degree of spinescence which is not a particularly common trait among the species recorded in this study. In fact, in this analysis Corelissen et al.'s (2003) spiney subcategories were merged into one simple spinescence category because of the low numbers in each group (Corelissen et al., 2003). Milton (1990) suggests that the more prickly spines found on species such as *Berkeya spinosa* and species of Ruschia have evolved as a defence against small browsers, but do not serve as protection against domestic livestock such as sheep and goats (Milton, 1990b). In a grazed plant community, those individuals with sturdier spines can serve as refugia for the safe establishment of other species (Milton, 1990b; Todd, 1999). Combined with autochory, this can increase the competitive pressure for establishment sites around a parent plant, further challenging these species in response to grazing pressure. Plant functional type 4 has a number of typical arid system traits, but these same traits do not stand up well to intense grazing and this group is a typical grazing 'decreaser' (Noy-Meir et al., 1989).

In examining responses across the fence line, plant functional type 1 was indeed a 'neutral' response group. This 'neutral' status was assigned on the basis of the combination of smaller stature with moderate palatability. Plant functional type 3 did not fulfil its predicted 'decreaser' status. It was assigned 'decreaser' status on the basis that it is a group of medium sized shrubs with a high degree of palatability, elements to align it with 'decreasers' in previous studies. However, it has lots of flowers and wind dispersed seeds. These traits must serve to counter balance the other more obvious and repeatedly recorded 'decreaser' traits. Plant functional type 3 is apparently a 'neutral' species. The failure of this plant functional type to agree with the predicted model demonstrates the significance of the traits to be included in a study in determining the outcome. This is further supported by plant functional type 1 which does not show a grazing response across the fence line on the basis of the traits selected here, but in considering its response across altitude, where other associated traits must come in to play, a response is evident.

The suggestion that plant functional types be sought within growth form groups gave no additional insight in this analysis (Lavorel et al., 1997; Landsberg et al., 1999). The findings to date agree with previous work that most plant functional types are primarily governed by growth form. In contrast to the suggestions of previous authors, this study points rather to a simplification in *only* considering growth form, where the inclusion of additional traits may have served to dilute the analysis. This is discussed further in considering the value of the adopted approach generally.

5.4.3 The examination of traits for additional insights

The consideration of traits alone gave some clear responses. The increase in long basal growth forms in response to grazing, for instance a number of the ground hugging succulents such as *Carpobrotus edulis* and *Mesembryanthemum chrystallinum* fits the global models where grazing favours more prostrate species (McIntyre and Lavorel, 2001; Diaz et al., 2007). These species have the ability to colonise space opened up through grazing simply through lateral spread, making this an obvious grazing 'increaser'

trait. The increase in erect leafy growth forms, which in this study included semi-basal species, is also previously, though not as commonly, recorded (Landsberg et al., 1999). This trait is largely inclusive of the traits of small stature and frequently annual or herbacecous plants and in its capacity to group these characteristics which are more commonly recorded 'increaser' traits, it takes on 'increaser' status.

Taller plants are common grazing 'decreasers' and the loss of medium height as a trait in response to sustained grazing is anticipated. Plant height generally gives plants a competitive advantage (Tilman, 1982; Weiher et al., 1999). However, there is a high cost to the investment in supportive structures necessary for space utilization (Lehsten and Kleyer, 2007) and as these 'expensive' structures are lost through grazing, combined with slow regeneration rates, the trait of height is selected against under high grazing pressure. Diaz et al. (2001) and Kleyer (1999) found plant height the best single predictor of grazing response (Kleyer, 1999; Diaz and Cabido, 2001). The fact that the trait 'tall' did not come up as a significant grazing 'decreaser' trait may be because most of the tall species such as *Olea europaea* and *Diospyros glabra*, are confined to the upland habitats, where water capture is greater allowing the establishment of taller species, and which are less heavily grazed (Petersen et al., 2004; Samuels et al., 2007) (see also Chapter 4).

Simple leaves is not a frequently used trait in plant functional type studies, and no previously recorded grazing response was found. Its status in this study as a 'decreaser' trait is attributed to the nature of grazing. A tug by a grazer on a simple leaf may be more devastating as the whole leaf is likely to be lost, or at least heavily damaged; whereas on a compound or lobed leaf only a portion of the leaf may be lost. Because leaves are essential for light interception, water and carbon dioxide balance, and ultimately photosynthesis and survival, a loss of leaves will impact a plant's success (Werger and Ellenbrok 1978). Leaf size, or as proposed here what remains of the leaf after it has been partially grazed and its associated functioning, relates to growth rate and therefore competitive ability (Garnier et al., 1997; Wright and Westoby, 1999; Lehsten and Kleyer, 2007). The 'character' of grazing here, as suggested by Fernandez et al. (1993), is shown to be an important consideration (Fernandez et al., 1993).

Flower number, also not a commonly incorporated trait in plant functional type studies, was included in this study as flowers are frequently the first element grazed off a plant, with an associated loss in reproductive success (Milton, 1994; Todd, 1999). This is borne out by the finding that the trait of few flowers is a 'decreaser' trait. This is interesting as work in the same area by Todd (1999) showed that those species with fewer, more conspicuous flowers were preferentially grazed. However, one cannot assume that a greater number of flowers is automatically associated with greater conspicuousness. However, even if this is the case, the higher the number of flowers means that under high grazing pressures species with more flowers are likely to have some reproductive success where those with few are at greater risk. Grazing tends to favour the proliferation of species with small seeds, and small seed size in turn is commonly correlated with higher numbers of flowers (McIntyre and Lavorel, 2001). This study suggests that limited reproductive output of few flowers, with possibly high investment in larger seeds, is a risky strategy in the face of intense grazing pressure. While there is more scope for work directly linking flower number and seed size, this study shows that flower number, a more readily measurable trait than seed size, is a useful grazing response trait.

The fact that palatability did not emerge as a grazing response trait was unexpected. An increase in unpalatable plants was anticipated as these species often proliferate in the absence of competition from palatable species. Palatability was important in a number of the plant functional type groupings where for example functional type 2 had a high number of palatable species, and functional type 4 a high number of unpalatable species, but not as a response trait. This is attributed to the fact that palatability is hard to measure and in some instances where palatability was unknown a middle value was assigned to a species possibly diluting the results. In addition to this, palatability is noted as a plastic trait which can vary between areas (Skarpe, 1996; Eviner and Chapin, 2003). For example in this study the species *Galenia africana* largely known to be unpalatable, is

described as palatable on the lower western, more coastal plains of Namaqualand (Schreuder, pers comm.).[3]

5.4.4 Plant functional types in response to grazing across altitude

The suggestion that sustained heavy grazing degrades an environment in such a way that it becomes equivalent to a more arid environment, is supported by the fact that there is a greater cover of plant functional type 1 at the highest altitude on the communal range (Hoffman and Cowling, 1990; Landsberg et al., 1999). The loss of plant cover, in particular perennials, results in bare patches which in turn has consequences for soil moisture through increased wind evaporation and ultimately affects soil nutrient status (Golluscio and Sala, 1993). Plant functional type 1 is succulent dominated, and while succulents do grow at these higher altitudes, they are more common to the lower, more arid western and eastern slopes of the Kamiesberg (see Chapter 3) (Mucina and Rutherford, 2006). The relatively higher proportion of plant functional type 1 on the communal range at higher altitudes suggests a change in environment here reflected in this biogeographic shift with more typically karroid elements on the communal range adjacent to moister Renosterveld on the private range. The altered environment acts as a selective force in terms of recruitment and survival where more typically arid species have a better chance of colonising open spaces (Sala et al., 1999; Gondard et al., 2003). Succulents tend to be shallow rooted and can access water from the shortest rain storms, giving them a competitive advantage on these possibly drier soils (Sala et al., 1999). This type of biogeographic shift is described in the literature as indicative of land degradation or alteration (Hoffman and Cowling, 1990). The fact that this biogeographic shift is evident on the uplands shows that the upland habitats are indeed grazed, even though less heavily, to the extent that these plant communities do show a grazing response. The upland habitats do not present a total safe zone and cannot be considered a repository of species for conservation purposes. The failure to detect a similar response on the lowland habitats is attributed to the fact that succulents at these altitudes are largely restricted to

[3] Mr Gawie Schreuder owns a farm in the heart of the Kamiesberg as well as one on the coastal plains to the west.

the rocky upland habitats where the threats of fire and competition are less (see Chapter 3).

5.4.5 The potential for developing indicator types

The complexity of issues and challenges around measuring land alteration and the various plans put forward to halt it are hinged on the need for simple indicator tools to measure and monitor alteration and restoration (Gray, 1999; Gondard et al., 2003; Cousins and Lindborg, 2004). Much of the work on plant functional types has been in search of just such grazing indicators (Noy-Meir et al., 1989; Navarro et al., 2006; Diaz et al., 2007). For a plant functional type to work as a monitoring tool it must be readily visible and easy to measure in the field (Cousins and Lindborg, 2004). The plant functional types generated in this study do serve to give some interesting insights into ecosystem function. However, as monitoring tools they would be too 'fuzzy' particularly where readily visible traits such as growth form are not always consistently grouped. Even the possible use of simple traits is complicated as one trait may relate to a number of functions, which in turn vary independently from one another (Weiher et al., 1999; Eviner and Chapin, 2003). For example the trait 'life history' can be related to functions such as space holding capacity, longevity, or even disturbance tolerance (Weiher et al., 1999).

A number of authors have searched for the optimal subset of traits which could be used in the generation of indicator types (Hodgson et al., 1999; Pillar, 1999; Weiher et al., 1999). This search, rather than giving us a universally useful subset, has served rather to highlight the complexity of grazing where optimal functional traits are best selected in relation to each specific purpose (Skarpe, 1996), and the importance of the categories used, and qualifications of subcategories is highlighted. Fernandez et al. (1993) note the variability of grazing itself and suggest that the 'character' of grazing needs to be better defined in adopting a plant functional type approach (Fernandez et al., 1993).

The filters acting on any plant community include climate, evolutionary history, disturbances and species interactions (McIntyre and Lavorel, 2001; Reich et al., 2003). Lavorel et al. (1999) and Diaz et al. (2007) highlight the significance of the influence of

climate and evolutionary context. At the end of his study of plant functional types in the species rich Fynbos, Bond (1999) warns against the oversimplification of a system through adopting a plant functional type approach, where one trait may have multiple imperceptible functions and one cannot make assumptions about functional redundancy (Bond, 1999). Several authors acknowledge this complexity and call for the creation of syndromes, which are not just isolated traits but rather a collection of meaningful traits which in turn relate to plant strategies (Lavorel et al., 1999; Reich et al., 2003). Eviner and Chapin (2003) suggest a functional matrix approach allowing for greater complexity in individual species' responses.

5.4.6 The value of a plant functional type approach for the Kamiesberg area

This plant functional type analysis does produce an informative typology for the study area and some grazing responses are evident. These are largely in agreement with the findings of the growth form analysis of Chapter 4 and numerous other grazing disturbance studies, and point towards the loss of longer lived woody perennials in favour of a community of fast growing annual and herbaceous plants. Once again what is evident in response to the sustained heavy grazing on the communal rangeland is an emerging altered plant community, comprising more ephemeral species and may respond variably to environmental perturbation (Diaz and Cabido, 2001). This analysis confirms the generally convergent trends of numerous previous plant functional type studies of a growth form based classification (Lavorel et al., 1997). However, the findings in this analysis are not as strong or as clear as those generated in the simple growth form analysis adopted in Chapter 4. The plant functional type analysis used in this study provides thought provoking results, and is informative in providing a framework to examine functioning. Nonetheless, the overall emerging results point to 'fuzzy' groups and not one of strong trait patterns (Landsberg et al., 1999). There may be a case for the selection of a different suite of traits. There is most certainly a problem on the continuum of traits, and the drawing of what may seem to be arbitrary lines in quantifying them (McIntyre and Lavorel, 2001; Eviner and Chapin, 2003). Each system falls within certain parameters, where for example the majority of the species of the Succulent Karoo may be shorter than a global species pool and by adopting the proposed universal language, so

strongly advocated by Corelissen et al. (2003), it is likely that too broad a brush was used and some responses were lost in the process. The search for a 'universal language' is contestable. Indeed in comparing the clearer findings of the growth form analysis of Chapter 4, and those of this study, the inclusion of additional traits, qualified in a one-size-fits-all manner, only served to dilute the results. In light of this there is a stronger case for the simple growth form analysis adopted in Chapter 4.

6. THE IMPACT OF SUSTAINED GRAZING ON STANDING PLANT BIOMASS

Abstract: This chapter presents estimates of the standing perennial biomass for the different vegetation types and associated habitats across the Kamiesberg. The impact of sustained heavy grazing associated with the communal rangelands on this plant biomass is then explored. Volume-biomass regressions, established for 94 perennial species accounting for 70 – 80% of the plant cover, are used in estimating standing perennial biomass. This study demonstrates the important role of environmental variability in producing the highly heterogeneous biomass across the Kamiesberg. Sustained heavy grazing is shown to significantly reduce biomass on the communal range on the accessible sandy lowlands, demonstrating the susceptibility of these habitats to alteration. The loss in biomass is principally of palatable species, with no evidence of a response in terms of perennial biomass, although the proliferation of annuals on the open ground of communal rangelands is well documented. A methodological examination of the potential to group species architecturally and develop generic regression curves for more widespread biomass studies proved unfeasible, demonstrating the unique intraspecific nature of allometric relationships.

6.1 INTRODUCTION

Plants accumulate biomass in response to biotic and abiotic drivers in the environment (Northup et al., 2005) (see also Chapter 3). Frequently used in ecosystem process modelling, be it in the examination of available forage, primary production, nutrient pools, species dominance, responses to experimental manipulation or in establishing fuel loads (Le Houerou et al., 1988; Navar et al., 2004; Soares and Schaeffer-Novelli, 2005), plant biomass is described as 'a metric fundamental to understanding and managing ecosystems' (Northup et al., 2005). Currently biomass assessment is receiving growing attention in the literature in response to research into carbon sinks in light of elevated carbon dioxide levels (Luo et al., 2002; Navar et al., 2004).

In assessing the state of any rangeland, biomass is an obvious measure. Plant biomass translates to available forage, and a significant loss in biomass in turn affects livelihoods (Reynolds and Stafford Smith, 2001). A reduction in biomass is described as a common feature of land degradation (Prince, 2001), or in this study what is more simply termed alteration. In this study, which examines the response of the vegetation of the Kamiesberg to sustained heavy grazing, a detailed understanding of standing plant biomass as a resource is important; both from a livelihood and a

conservation standpoint. An understanding of perennial biomass tells us of the *status quo* of a system, the effects of past impacts, and can elucidate ecological responses and dynamics, all of which in turn feed in to livelihood and conservation management considerations. The combination of altitudinal gradient and variable land-use has allowed for an examination of standing plant biomass in this study across both a natural and human-induced gradient.

There is considerable scope for expanding our knowledge of plant biomass in different vegetation types, and for improving measurement techniques (Navar et al., 2004). The accurate assessment of plant biomass is difficult, where the area to be covered, the nature of the vegetation, the question to be addressed, and inevitable time and financial constraints, all influence the method to be adopted and the degree of accuracy achieved (Catchpole and Wheeler, 1992; Keller et al., 2001). Numerous techniques are available such as through remote sensing (see Chapter 7), destructive sampling, and the use of allometric relations. Accuracy in measuring biomass is described as paramount where a detailed understanding of available forage is vital for rangeland management decisions and environmental sustainability (Le Houerou et al., 1988). Methodologies based on extensive destructive sampling are increasingly hard to justify, as well as being expensive and time consuming (Navar et al., 2004). This study used a method based on the allometric relationship between plant volume and biomass, to estimate standing biomass in the six different vegetation types across the Kamiesberg Mountain range. Work in the forests of Brazil have shown the use of allometrically derived equations to be extremely effective (Keller et al., 2001). Indeed, the use of allometrically-derived equations is described as highly effective, with low error and the added advantage of allowing the sampling of large areas with relative ease (Haase and Haase, 1995; Guevara et al., 2001; Mani and Parthasarathy, 2007). The success of the methodology used is reviewed and the potential to contribute to future standing perennial biomass studies is explored.

This study addresses the following specific questions:

1. How does standing biomass vary between the different vegetation types across the Kamiesberg?
2. Has the sustained heavy grazing associated with the communal range significantly affected standing biomass?

3. Does biomass vary in terms of palatability in response to the sustained heavy grazing on the communal range?
4. Does the method provide an accurate and efficient measure of biomass?
5. Can volume-biomass relationships be generalised across certain groups of plant species?

6.2 METHODS

6.2.1 Study site

This study was conducted across the boundary of the Leliefontein communal area and the immediately adjacent, privately-owned farms. For details of the study site see Chapter 2.

6.2.2 Data collection

Species cover data were collected for all species in 66, 20X50 m Whittaker plots, situated on either side of the fence and across a range of rocky-upland and sandy-lowland habitats (see Chapter 3). A list of those species accounting for 70 – 80% of the perennial cover was created. A volume-biomass regression curve was generated for each of these species by sampling six individuals of a range of sizes (Catchpole and Wheeler, 1992). A diversity of sizes was used in order to best capture the full range of the volume-biomass relationship for each species. Three individuals of each species was then oven-dried at 60ºC for three days to establish a wet:dry ratio. In order to gain a mean volume for the dominant species at each sample site, height and two diameter measures were taken from ten individuals selected at random of those species dominating cover at that site (Catchpole and Wheeler, 1992). Sampling was carried out in the spring of 2003 and 2004. No two species were sampled in consecutive years, rather those few species not collected in 2003 where then sampled in 2004.

6.2.3 Establishment of mean biomass at each site

Based on the assumption that most shrubs can be represented as an oblate spheroid (Philips and MacMahon, 1981), the mean cross-sectional area of individuals as measured at each site was established. The area was then divided (generated from the

percentage area occupied) by the mean cross-sectional area to establish mean number of individuals per $1m^2$. This was then multiplied by the mean volume for that specific species at that site. Using this volume, the associated biomass values were then worked out through the relevant regression equation (as generated by a range of species off site) (Flombaum and Sala, 2007). In a few instances data for individual species were log-transformed, improving the significance of the volume-biomass regression (marked with asterisk (*) in Table 6.1). This was in turn converted to dry biomass. After adding all species for a particular site accounting for 70 – 80% of the cover, this was extrapolated to dry mass for 1 hectare. For general data measures across the Kamiesberg private data are used as a proxy for a 'natural' system, since these lands are less heavily stocked (Todd and Hoffman, 2000). Communal data are used for consideration of the grazing impact only.

6.2.4 Examining palatability

Species were attributed palatability ratings (1 = unpalatable, 2 = moderately palatable, 3 = highly palatable) based on available literature and expert knowledge. Expert knowledge was obtained from local herders and botanists who are active in the Kamiesberg area. Biomass for each site was then categorised accordingly and the unpalatable, moderately palatable and highly palatable biomass established.

6.2.5 Statistical analyses

In examining differences between vegetation types, and between upland and lowland habitats, data were found to be non-normal and the Mann-Whitney-U test for non-parametric data was used to test for significant differences. A paired Wilcoxon sign-rank test was used to test for significant differences in total biomass and biomass graded according to palatability on either side of the fence. Multiple comparison of means tests were used for a post-hoc comparison in the case of non-parametric tests.

To examine the potential of using established volume-biomass regressions for further research, ANCOVAs and tests for homogeneity of slope and elevation were used. Species were initially allocated one of the following growth and architectural forms: herbaceous shrub, grass, dwarf shrub (< 25 cm), dwarf succulent shrub (< 25 cm), woody shrub (> 25 cm) and succulent shrub (> 25 cm). In instances where data were non-normal, where visual assessments pointed to obvious sub groupings, or where no

patterns were found, smaller groups based on genera or more specific architectural aspects, were analysed.

6.3 RESULTS

6.3.1 Biomass for different vegetation types

A total of 94 species was sampled and volume-biomass regressions, and wet: dry weight ratios, generated (Table 6.1).

Table 6.1 Regression equations, r^2 values and percentage dry weight for the species sampled. In the regression equation x presents for volume and y biomass. Species are grouped according to growth form. Data that were log transformed are indicated with an asterisk (*).

Species	regression equation	r^2	% dry weight
Herbaceous shrub			
Aizoon canariense L.	y = 532923x + 0.5964	0.89	28.2
Asparagus capensis L.	y = 4395.2x + 4.5642	0.74	76.4
Galenia sarcophylla Fenzl	y = 0.4471x + 3.1549*	0.63	59.0
Hypertelis salsoloides (Burch.) var. salsoloides Adamson	y = 115153x + 9.6987	0.84	38.6
Manochlamys albicans (Aiton) Aellen	y = 4487.7x + 3.5634	0.79	81.8
Restio cymosus (Mast.) Pillans	y = 3361.7x + 89.513	0.74	75.4
Tetragonia fruiticosa L.	y = 4054.2x + 2.5351	0.89	23.4
Grass			
Chaetobromus involucratis (Schrad.)Nees subsp dregeanus(Nees)Verboom	y = 5280.3x + 82.432	0.76	76.7
Ehrharta barbinodis Nees ex Trin.	y = 11.323x + 32.687	0.77	69.5
Fingerhuthia africana Lehm.	y = 12272x + 20.947	0.79	73.9
Merxmuellera stricta (Keller and Schradin) Conert	y = 1659x + 91.987	0.77	77.7
Pentaschistis barbata (Nees) P.H.Linder subsp. Barbata	y = 264112x + 22.319	0.81	89.2
Stipagrostis brevifolia (Nees) DeWinter	y = 15500x + 27.656	0.87	73.8
Dwarf shrub			
Blepharis furcata (L.f.) Pers.	y = 4871.3x + 13.547	0.92	64.0
Chrysochoma cilliata	y = 2540.8x + 39.336	0.6	51.1
Hirpicium alienatum (Thunb.) Druce	y = 1563.9x + 34.874	0.68	51.5
Indigofera heterophylla Thunb.	y = 11706x + 12.666	0.82	78.5
Lobostemon glaucophyllus (Jacq.) H.Buek.	y = 5704x + 182.49	0.82	57.0
Oftia revoluta (E.Mey.) Bocq.	y = 5466.9x + 228.8	0.95	32.5
Pentzia incana (Thunb.) Kuntze	y = 16049x + 10.597	0.97	78.9
Phylica montana Sond.	y = 10541x - 367.71	0.91	79.7
Selago multiflora Hilliard	y = 4782.3x + 313.47	0.94	87.5
Selago scabribracteata Hilliard	y = 6446.9x - 535.65	0.89	72.8
Senecio cinerascens	y = 4779.2x - 6.8515	0.79	30.9
Dwarf succulent shrub			
Antimima compacta (L.Bolus) H.E.K.Hartmann	y = 140469x + 24.56	0.56	34.8
Antimima pusilla	y = 120389x - 1.4088	0.71	54.8
Antimima spp.	y = 78913x - 107.63	0.96	53.3
Cephalophyllum ebracteatum (Schltr. & Diels) Dinteer & Schwantes	y = 163990x + 144.63	0.66	21.8
Cheiridopsis denticulata (Haw.) N.E.Br.	y = 310291x + 65.771	0.89	32.9
Cheiridopsis namaquensis (Sond.) H.E.K.Hartmann	y = 912116x + 33.045	0.65	58.1
Conicosia elongata (Haw.) N.E.Br.	y = 49839x + 42.061	0.73	11.8
Drosanthemum brevifolium (Aiton) Schwantes	y = 18253x + 47.235	0.88	27.6
Drosanthemum hispidum (L.) Schwantes	y = 823515x - 19.775	0.75	21.5
Drosanthemum oculatum L.Bolus	y = 21790x + 107.55	0.94	40.0
Drosanthemum schoenlandianum (Schltr.) L.Bolus	y = 65894x + 3.0603	0.97	24.0
Ruschia fugitans L.Bolus	y = 0.9169x + 5.1773*	0.73	33.5
Ruschia macownii = Ruschia kheis	y = 116870x + 1.9418	0.88	18.8
Ruschia viridifolia L.Bolus	y = 95979x + 69.664	0.97	26.2
Succulent shrub			
Antimima subtruncata (L.Bolus) H.E.K.Hartmann	y = 15353x + 328.71	0.71	14.1
Aridaria brevicarpa L.Bolus	y = 15528x + 262.42	0.78	45.2
Euphorbia decussata E.Mey. Ex Boiss.	y = 26038x + 12.354	0.69	31.2
Euphorbia mauritanica L. var. mauritanica	y = 1.0126x + 4.6422*	0.89	20.4
Kleinia longiflora DC.	y = 8797.9x + 1238	0.79	29.4
Lampranthus otzenianus (Dinter) Friedrich	y = 9724.1x + 102.72	0.66	62.9
Leipoldtia laxa L. Bolus	y = 74901x + 8.9878	0.96	18.7
Leipoldtia schultzei (Schltr. & Diels) Friedrich	y = 9781.6x + 29.739	0.89	33.5
Othonna floribunda Schltr.	y = 1584.3x + 776.93	0.96	71.8

Polymita albiflora (L.Bolus) L.Bolus	y = 129243x + 41.199	0.6	40.5
Ruschia brakdamensis (L.Bolus) L.Bolus	y = 13119x - 47.819	0.84	32.5
Ruschia crassisepala L.Bolus	y = 23391x + 449.2	0.75	43.7
Ruschia goodiae L.Bolus	y = 0.8068x + 4.6016	0.85	25.1
Ruschia lerouxiae (L.Bolus) L.Bolus	y = 17717x + 26.772	0.81	26.1
Ruschia robusta L.Bolus	y = 6331x + 17.256	0.85	43.8
Ruschia stricta L.Bolus	y = 21735x + 3.1932	0.99	15.4
Stoeberia beetzii (Dinter) Dinter & Schwantes	y = 9133.3x + 1616.5	0.85	23.5
Zygophyllum cordifolium L.f.	y = 0.7856x + 3.9548*	0.72	63.1
Zygophyllum morgsana L.	y = 16003x + 132.38	0.96	45.7
Zygophyllum retrofractum Thunb.	y = 45086x + 218.77	0.71	50.6
Woody shrub			
Antizoma miersiana Harv.	y = 2408.4x + 578.88	0.69	66.6
Berkheya spinossisima (L. f.) Druce	y = 2101.1x + 38.691	0.96	38.2
Cadaba aphylla (Thunb.) Wild	y = 9820.9x + 429.98	0.82	73.2
Cliffortia ruscifolia L. var. ruscifolia	y = 2231.4x + 77.175	0.64	82.9
Clutia thunbergii Sond.	y = 8993.9x + 379.52	0.95	87.8
Coleonema juniperinum Sond.	y = 1669.6x + 481.68	0.54	55.1
Dicerothamnus rhinocerotis (L. f.) Koekemoer	y = 1128.5x + 787.09	0.83	78.3
Didelta spinosa (L.f.) Aiton	y = 2633.4x + 393.78	0.87	70.4
Dimorphotheca cuneata (Thunb.) Less.	y = 8933.1x - 90.705	0.84	80.3
Diospyros glabra (L.) De Winter	y = 3523.3x + 57.691	0.85	83.4
Dodonaea viscosa Jacq. var.angustifolia	y = 1110.7x + 925.16	0.88	74.0
Dyerophytum africanum Kuntze	y = 2376.5x + 310.38	0.72	78.4
Eriocephalus ericoides (L. f.) Druce subsp. Ericoides	y = 10434x + 0.1569	0.84	74.6
Euryops laterifolius (L.f.) DC.	y = 0.8035x + 3.8035	0.98	67.9
Galenia africana L.	y = 4249.2x + 12.525	0.93	71.9
Hermannia cuneifolia Jacq. Var. cuneifolia	y = 1603.7x + 10.337	0.81	85.7
Hermannia disermifolia	y = 9422.9x + 3.4742	0.97	68.6
Hermannia rigida Harv.	y = 1357.1x + 167.04	0.95	70.8
Hermannia sp. Kheis	y = 3953.5x - 23.962	0.98	54.6
Hermannia trifurca L.	y = 11773x - 1.0807	0.99	48.4
Indigofera nigromontana Eckl. & Zeyh.	y = 4363.7x + 77.924	0.86	78.4
Lebeckia cinerea E.Mey.	y = 1.0595x + 3.5001*	0.75	56.2
Lebeckia multiflora E.Mey.	y = 5190x + 227.51	0.77	59.1
Lycium ferocissimum Miers	y = 11703x + 58.846	0.92	59.6
Monechma spartioides (T.Anderson) C.B. Clarek	y = 6446.9x - 535.65	0.89	72.8
Montinia caryophyllaceae Thunb.	y = 2273.1x + 50.588	0.89	70.6
Oederoa genistifolia (L.) Anderb. & K.Bremer	y = 2235.5x + 124.55	0.88	74.2
Pteronia incana (Burm.) DC.	y = 8170.7x - 337.05	0.71	72.4
Pteronia inflexa Thunb. Ex L.f.	y = 7733x - 98.24	0.76	90.3
Rhus horrida Eckl. & Zeyh.	y = 4352.1x + 7.6304	0.98	83.3
Rhus incisa L. f. var. effusa (C.Presl) R.Fern.	y = 4555.3x + 259.03	0.91	78.6
Rhus undulata Jacq.	y = 5638x + 70.118	0.93	67.9
Salsola grey tight leaves	y = 24201x + 9.1697	0.98	68.2
Stachys rugosa Aiton	y = 429.29x + 26.265	0.63	65.4
Struthiola leptantha Bolus	y = 3380x - 87.856	0.86	81.6
Tripteris sinuata DC. Var. sinuata	y = 6638.9x + 26.273	0.92	49.6

Standing perennial biomass for the lowland areas of the private rangeland ranged from 3292 kg per hectare for a Heuweltjieveld site to 19780 kg per hectare for a Renosterveld site. Upland equivalents ranged from 3728 kg per hectare for a Western klipkoppe site to 25645 kg per hectare for a Mountain shrubland site (Figure 6.1). Total biomass varied significantly across all sites ($n = 32$, $H = 19.02$, $p < 0.005$).

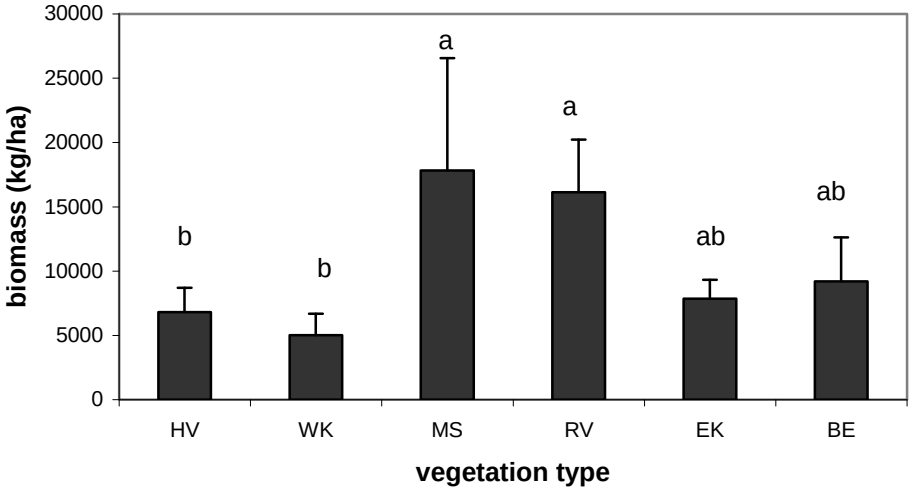


Figure 6.1 Mean standing perennial biomass for six vegetation types (±SD) (upland and lowland sites combined, private lands only), organised in a west-east direction along the x-axis, across the Kamiesberg Mountain range (HV = Heuweltjieveld, WK = Western klipkoppe, MS = Mountain shrubland, RV = Renosterveld, EK = Eastern klipkoppe, BE = Bushmanland ecotone). Post-hoc comparisons, indicated with superscripts, are based on a multiple comparison of means test.

The dwarf succulent shrub *Conicosia elongata* had the highest moisture content at 88% of its total weight and the woody shrub *Pteronia inflexa* had the lowest at 9.7%. The ratio of wet to dry weight varied considerably across the different growth forms. Mean moisture content as a measure of plant weight in herbaceous shrubs was 45% (±SD = 24, n = 21), for grasses was 23% (±SD = 6.7, n = 18), for dwarf shrubs was 38% (±SD = 19, n = 33), for dwarf succulent shrubs was 67% (±SD = 14, n = 40), for succulent shrubs was 63% (±SD = 16, n = 60) and for woody shrubs was 29% (±SD = 12, n = 102).

6.3.2 Biomass contrasted between lowland and upland sites

Perennial standing biomass as measured on the sandy lowland areas was consistently less that the rocky upland equivalent in each vegetation type (Figure 6.2) (n = 32, H =

7.08, p <0.005). A Tukey's Honest Significant Difference test showed no significant differences between lowland and upland biomass within vegetation types. Comparisons within habitat type also varied significantly (lowland: n= 15, H = 10.4, p < 0.05, uplands: n = 17, H = 12.14, p < 0.05). A multiple comparison of means showed this difference in both the lowland and uplands to lie between the Western klipkoppe and Renosterveld vegetation types for the lowlands and the uplands, with the addition of difference between Western klipkoppe and Mountain shrubland for the uplands.

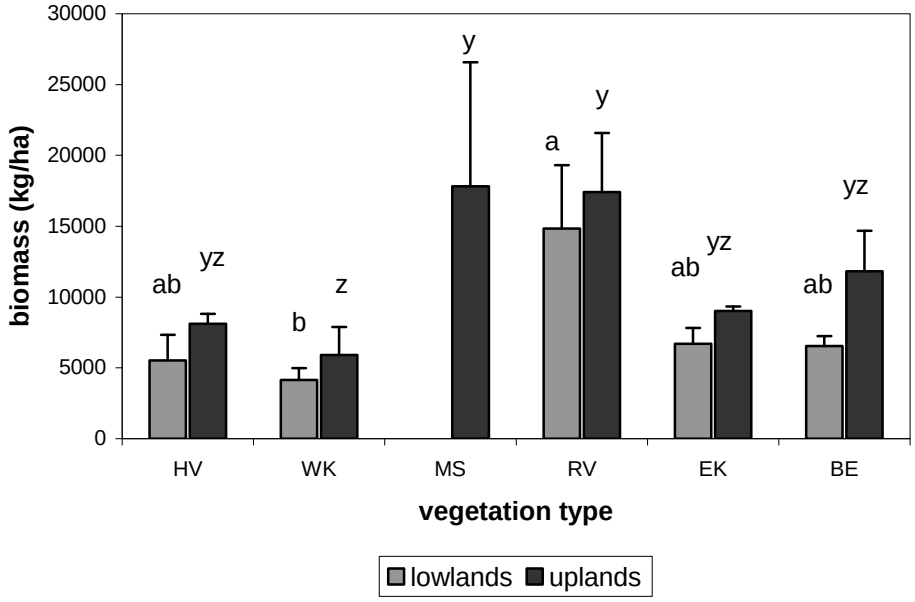
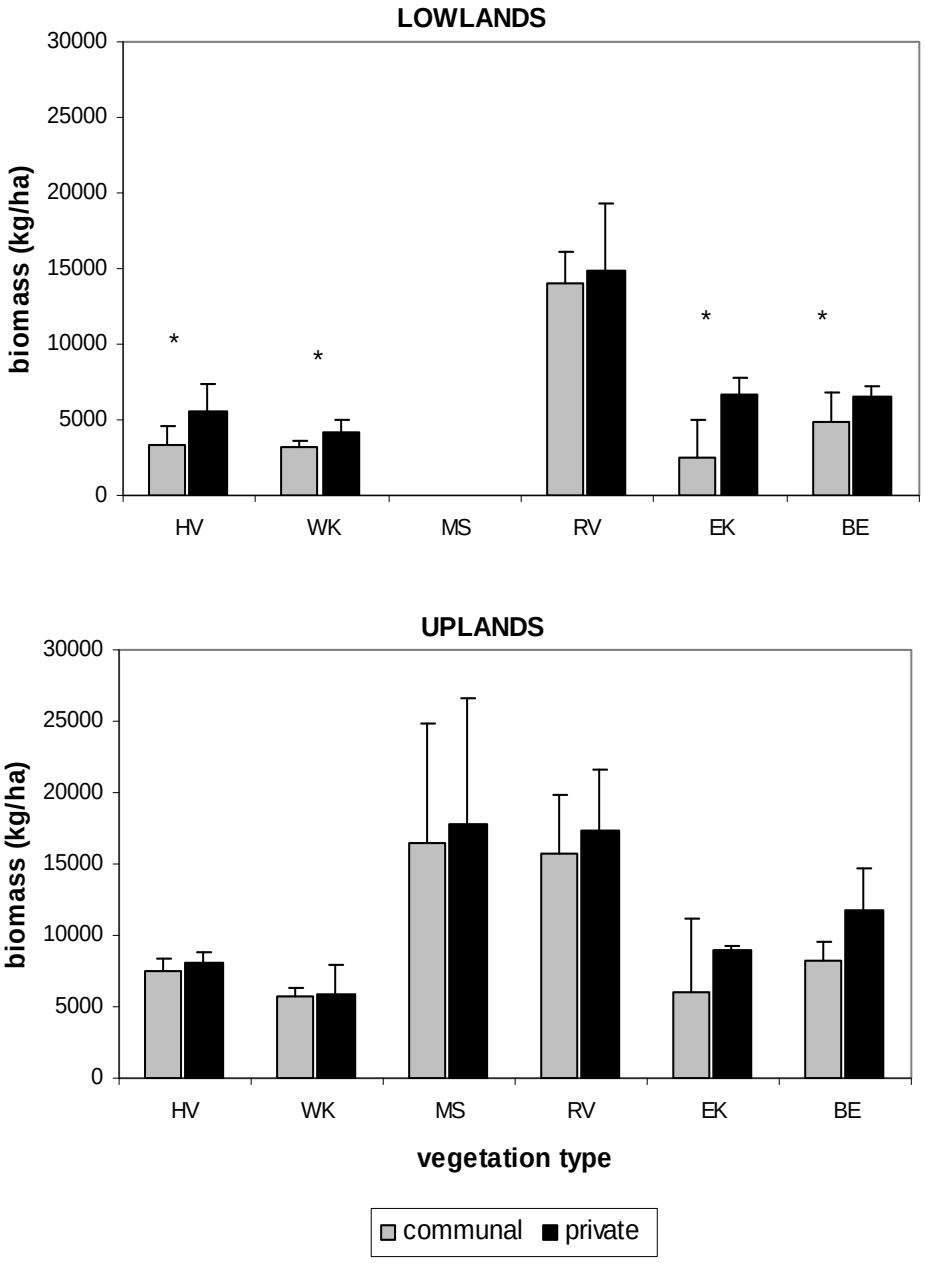


Figure 6.2 Mean perennial standing biomass (±SD), for lowland and upland components of the vegetation different types across the Kamiesberg Mountain range (HV = Heuweltjieveld, WK = Western klipkoppe, MS = Mountain shrubland, RV = Renosterveld, EK = Eastern klipkoppe, BE = Bushmanland ecotone). Post-hoc comparisons, indicated with superscripts, are based on a multiple comparison of means test, with a and b indicating significant differences on the lowlands, and y and z indicating significant differences on the uplands.

6.3.3 Biomass across the communal-private fence line

Biomass was consistently lower on the communal rangeland than the private rangeland (Figure 6.3). Communal lowland figures ranged from 459 kg per hectare for an Eastern klipkoppe site to 16216 kg per hectare for a Renosterveld site. Biomass figures for the communal uplands ranged from 1990 kg for an Eastern klipkoppe site to 22439 kg per hectare for a Mountain shrubland site. Biomass was significantly lower for all paired communal lowland sites (n = 33, T = 23.0, z = 2.101, p < 0.05).

This was with the exception of the Renosterveld where high variability on the private range rendered the data nonparametric and no significant difference was found. While the same trend appears to be evident on the uplands, the relationship was not significant.



Figures 6.3 Mean standing perennial biomass (±SD), for communal and private rangelands for six different vegetation types across the Kamiesberg Mountain range, for lowland and upland habitats (HV = Heuweltjieveld, WK = Western klipkoppe, MS = Mountain shrubland, RV = Renosterveld, EK = Eastern klipkoppe, BE = Bushmanland ecotone). Significant differences between paired sites in each vegetation types are indicated with an asterisk (*).

6.3.4 Palatability results

Highly palatable biomass was significantly higher on the private rangeland than the communal rangeland (T = 106.00, z = 2.60, p = 0.009) (Figure 6.4). Biomass of unpalatable and moderately palatable species did not differ significantly as a function of land use (Figure 6.5).

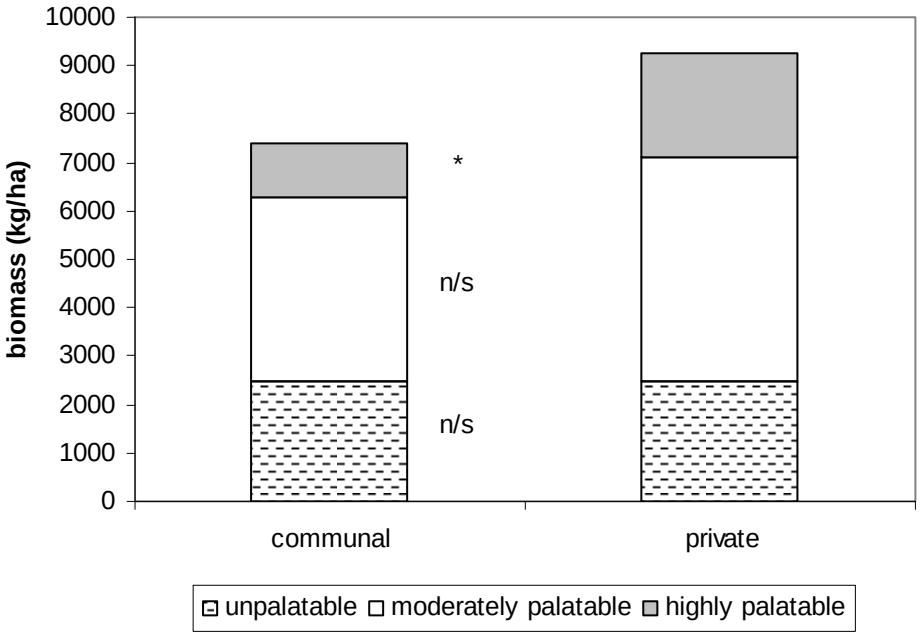


Figure 6.4 Cumulative standing perennial biomass of unpalatable, moderately palatable and highly palatable species on communal and private rangeland. Asterisk (*) indicates a significant difference at $p < 0.01$.

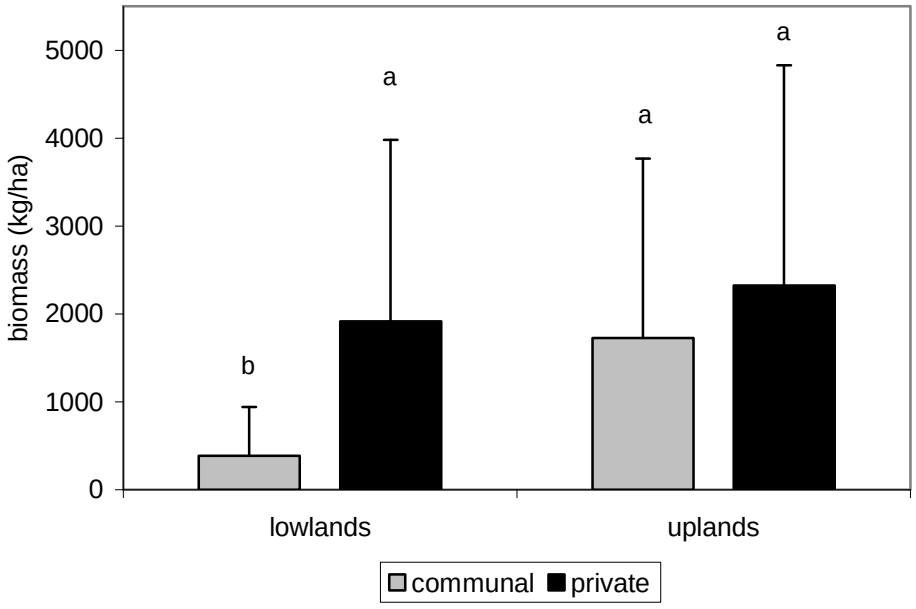


Figure 6.5 The distribution of highly palatable biomass on the communal and private range according to habitat type. Post hoc comparisons, indicated with superscripts, are based on a multiple comparisons of means test.

6.3.5 Generalisation of regression equations

No significant groupings were elucidated with regards to volume-biomass regressions. In a few instances where significant relationships were found, the grouping relationship was too tenuous to warrant reporting (for example two unrelated woody shrubs may share a regression slope and intercept, while a closely related shrub of similar architecture does not).

6.4 DISCUSSION

6.4.1 Perennial standing biomass of the Kamiesberg

The use of linear regressions based on allometric relationships established between biomass and an easily measured variable, in this instance volume, proved effective (Flombaum and Sala, 2007), with biomass estimates in keeping with other researchers' findings (Table 6.2) (Catchpole and Wheeler, 1992). Biomass for the Heuweltjieveld is in agreement with equivalent measures and Mountain shrubland and Renosterveld vegetation types fall in the middle of the range given for Fynbos (Werger and Morris, 1991; Richardson and Cowling, 1992). Measures for the Eastern

and Western klipkoppe are in some instances higher, some instances lower, and in the case of a Western klipkoppe measure, exactly the same as, equivalent measures (Werger and Morris, 1991; Carrick, 2005; O'Farrell, 2005). Biomass measured on the Bushmanland ecotone lowlands is considerably higher than the 'equivalent' measure given here taken from a Nama-karoo grassland site. This may be an inappropriate comparison where Skowno's (2003) measure is from the Great Karoo and Central Lower Karoo subdivision and characterised as an arid shrubland, while the site in this project falls in the Griqualand West and Bushmanland subdivision of the Nama-karoo biome characterised by arid grasslands (Palmer and Hoffman, 1997; Skowno, 2003). While measures are generally comparable, variability exists between measures in this study and those in the literature. Reasons for this can be explained by the use of different techniques, the heterogeneous nature of the Karoo vegetation and in particular the Kamiesberg vegetation, and the variable and imperfect nature of standing biomass measurements (Beatley, 1969). The range of values in the literature generally is large, and points to both the difficulty of measuring biomass and the high degree of variability in plant biomass.

Table 6.2 Biomass values from previous studies for comparative purposes.

Vegetation type	'Equivalent' vegetation type in current study	Biomass (kg / ha^{-1})	Author
Eastern Klipkoppe lowlands	Eastern klipkoppe lowlands	±2500	(Carrick, 2005)
Nama and Succulent Karoo Biomes	Broadly all vegetation types included in study	500 – 7600	(Rutherford and Westfall, 1986)
Nama Karoo	Bushmanland ectone lowlands	3449	(Skowno, 2003)
Tierberg	Eastern klipkoppe lowlands	3268	(Milton, 1990a)
Namaqualand coastal belt	Heuweltjieveld	8100	(Werger and Morris, 1991)
Western mountain Karoo	Western klipkoppe	5200	(Werger and Morris, 1991)
Dolerite koppie veld	Eastern and Western klipkoppe uplands	6000	(O'Farrell, 2005)
Mountain fynbos	Renosterveld and Mountain shrubland	15 000 – 51 000	(Richardson and Cowling, 1992)
Niewoudtville Karoo veld	Eastern and Western klipkoppe lowlands	12 000	(O'Farrell, 2005)

Interestingly, biomass is greatest not only at the wettest part of the Kamiesberg as perhaps anticipated (Noy-Meir, 1973), but on both the western slopes of the mountain, in the Mountain Shrubland vegetation and in the Renosterveld. The high

biomass in the Mountain Shrubland is likely to be a function of the combination of high rainfall, warmer temperatures and deeper soils than the rocky peaks (see Chapter 3). In examining primary productivity in semi-arid and arid systems, the role of smaller scale processes has been highlighted. Le Houerou et al. (1988) found that while annual and seasonal productivity was closely tied to rainfall, variability in productivity was 1.5 times higher than variability in rainfall. The relationship between productivity, or in this study standing biomass, and rainfall cannot be assumed to be linear (Le Houerou and Hoste, 1977; Ludwig, 1987; Le Houerou et al., 1988).

It was disappointing not to have been in a position to include annual cover which was negligible as a result of the low rainfall in both years of sampling. However, this is symptomatic of the region, where drought or the timing of rainfall means the production of annual cover is highly variable (Esler, 1999; Samuels et al., 2007). This variability is proliferated through the year as conditions will also affect reproductive allocation where annuals may germinate but have reduced reproductive output due to water stress later in the season (van Rooyen et al., 1991). Indeed the failure of annuals under certain rainfall conditions is described as a feature of semi-arid systems (Beatley, 1969; O'Connor and Roux, 1995). The fact that annuals could not be included in this study serves to demonstrate the importance of perennial cover for sustained grazing where annual cover cannot be depended on, supporting the view presented in Chapter 4 in light of compositional shifts in response to grazing, where a system that becomes more tightly coupled to rainfall potentially places farmers at greater risk.

The moisture content of species sampled is for the most part in keeping with the findings of Milton (1990) who collected and dried a number of species in the southern Karoo. The outer values in this current study were slightly lower, possibly a function of the time of sampling, where Milton sampled in winter. Plant moisture content is an important aspect of forage, influencing how frequently animals will need to access surface water (Owen-Smith, 1999). This is evident where stock keepers move stock posts closer to water points during the dry season and droughts (Hendricks et al., 2005). Succulents are described as making a significant contribution to animal water balance (Owen-Smith, 1999). With intense grazing pressure there may be a reduction

in, or complete loss of, species with high moisture content, and this aspect of biomass loss will in turn have implications in how pastoralists use the rangeland.

6.4.2 Biomass contrasted between lowland and upland sites

Plant composition is different on rocky upland areas as a function of environmental variables such as greater soil moisture due to run-on as a result of higher rock cover and elevated soil nutrient status (Ludwig, 1987; Burke, 2001; Petersen et al., 2004) (Chapter 3). The rocky upland areas are home to the limited tree species found in Namaqualand, such as several species of Rhus recorded in this study. While the extensive rock cover at each site means plant cover is less on the uplands, biomass is consistently greater. These steep rocky areas are also known to be less heavily grazed than their lowland equivalents due to their frequently inaccessible nature (Cowling et al., 1994; Riginos and Hoffman, 2003; Petersen et al., 2004; Pienaar et al., 2004; Samuels et al., 2007). The leaves of trees are noted for retaining water through dry periods, making them an appealing forage source for browsers, such as goats, during drought (Owen-Smith, 1999). These areas serve as key resource areas for use in the dry season or times of drought (Illius and O'Connor, 1999; Petersen et al., 2004; Samuels et al., 2007).

6.4.3 Biomass across the communal-private fence line

The sustained heavy grazing associated with the communal range is evident in the significant loss of biomass on the communal lowlands. This is in keeping with findings of losses of plant guilds with shifts from woody perennial dominated cover to smaller more ephemeral species on the communal range, both locally (Todd and Hoffman, 1999) (see also Chapter 4) and internationally (Fernandez-Gimenez and Allen-Diaz, 1999; Brathen and Oksanen, 2001; Hickman and Hartnett, 2002; Marcelo et al., 2003; Foroughbakhch et al., 2005). This may in turn have implications for those who depend on the natural vegetation for their livelihoods through stock farming (Dube and Pickup, 2001; Foroughbakhch et al., 2005; Reynolds et al., 2007). The fact that upland biomass on the communal range does not differ significantly from that of the private range corroborates the idea that the upland areas are buffered from the intense grazing pressure associated with the lowland areas, due to their less accessible nature (Petersen et al., 2004; Samuels et al., 2007) (see also Chapter 4).

6.4.4 Standing perennial biomass and palatability

There is considerable literature which demonstrates that sustained heavy grazing results in an increase in unpalatable plants where selective pressure indirectly favours co-occurring species through competitive release (West, 1993; James et al., 1999; Todd and Hoffman, 1999; Hickman and Hartnett, 2002; Riginos and Hoffman, 2003; Foroughbakhch et al., 2005; Diaz et al., 2007). This competitive release can be through reduced reproductive output as flowers or seed pods are grazed, reduced plant size and associated photosynthetic potential, or the complete removal of entire individuals (Hickman and Hartnett, 2002; Marcelo et al., 2003). The findings in this study confirm that the more palatable species are heavily utilized on the communal range, but contrary to what might be anticipated, do not show any evidence of an increase in unpalatable species. There are also reports of increases in the unpalatable species *Galenia africana* on the communal rangeland both anecdotally and in studies in the Eastern klipkoppe vegetation, but this is not evident in this study (Allsopp, 1999). It is possible that this species has a close association with old ploughed lands, which were excluded in this study (Allsopp, 1999). Recent work, also in the Eastern klipkoppe vegetation, shows a close association between *G. africana* and soil depth, perhaps limiting this reported grazing response to areas of deeper soils (Petersen, in prep.). The findings of this current study suggest a very static or sluggish system where there is the apparent loss of one suite of species with no evident community response.

Previous work in the area, and internationally, has shown that annual plants are favoured by this competitive release and proliferate in the open spaces generated by heavy grazing given good and well-timed rainfall (Todd and Hoffman, 1999; Diaz et al., 2007). While not measured in this study, this is apparently the response to grazing. While annuals present good forage quality, their very short-lived nature means that in attributing their overall grazing value they do not score particularly well (Todd and Hoffman, 2000; Botha et al., 2001). Botha et al. (2001), in establishing grazing index values for a number of karoo plants, incorporate a 'nutritional value during the dormant season', and 'degree of perenniality' scores, both of which greatly reduce the grazing index value of annual species. Annuals are described as sensitive to

disturbance. Studies from the Sahel show a shift from perennial grasslands to annual dominated vegetation in response to heavy grazing. The collapse of the annual 'forage' in response to low rainfall led to a period of famine, and desertification (van de Koppel et al., 1997). While annuals may present high forage quality, their presence is short-lived and unreliable. Small fluctuations in environmental parameters can lead to relatively large shifts in vegetation states, posing considerable risk to those depending on this resource for their livelihoods (van de Koppel et al., 1997).

The question remains as to why no perennial unpalatable species are filling the gap created by the heavy grazing on the communal range. It may be that the advantage of a higher and earlier reproductive response of the r-selected annual species allows them to out-compete perennial species in colonising available open ground (Grime, 2001). Work on grazing effects in Kansas prairies showed that perennial plants contributed only 3% to the seed bank, giving the annual species a significant competitive advantage (Marcelo et al., 2003). Work in serpentine grasslands in California demonstrated the competitive vigour of annual seedlings where high annual numbers significantly reduced bunchgrass biomass (Hooper, 1998). In this study area the lowland areas are described as heavily utilized during the growing season, in particular on the communal range, further limiting the success of those few perennial seedlings attempting to emerge or establish during this time (Petersen et al., 2004). Or it is possible that the nature of the semi-arid system, where water is the primary limiting factor, means competition is not a driving force. In this instance perennials would only be in a position to germinate and establish in particularly favourable conditions. However, this would be counter to the belief that the proliferation of unpalatable species in response to grazing is in fact more common in arid systems than humid ones (Diaz et al., 2007). Work on grazing by reindeer found the same results as in this study, where the only significant change in biomass was in the loss of highly palatable species (Brathen and Oksanen, 2001). In their study, and indeed in others, researchers attribute responses to the highly individual nature of plant responses to grazing. Plants are allocated to increaser and decreaser categories, described as falling on a continuum from negative to over-compensatory in response, and intraspecifically variable in their direct and indirect responses to grazing (Beatley, 1969; Brathen and Oksanen, 2001; Hickman and Hartnett, 2002; Jauffret and Lavorel, 2003; Marcelo et al., 2003). In addition to palatability, factors such as community

composition and associated interspecific variability in architecture, phenology, and local abundance may also vary (Hickman and Hartnett, 2002). A study looking at grazing by different native ungulates in shrubsteppe communities demonstrates the importance of the grazers in question, where different animals will graze plants variably (Rexroad et al., 2007). The nature of grazing is relevant in determining the type of community response (Fernandez et al., 1993). Evidently plant-herbivore interactions are complex, compounding the scope for ready interpretation and generalisations. Palatability, as a plant functional trait, is reviewed in more detail in Chapter 5.

The appearance of unpalatable species is a common indicator of degraded range condition (Owen-Smith, 1999). Whatever the driver, these findings demonstrate that in this system the absence of highly palatable species, rather than the presence of unpalatable species, would make a more effective rangeland condition indicator (Todd, 2006).

6.4.5 Methodological considerations

The measurement of biomass is problematic (Navar et al., 2004). Either it involves arduous and destructive methods with associated high costs and disturbance to study sites, or it becomes a more tenuous science involving some degree of speculation with implications for the degree of accuracy (Catchpole and Wheeler, 1992; Northup et al., 2005).

It is felt that the results obtained in this study are sufficiently in keeping with those of other researchers to lend support to the methods adopted here. Indeed this finding is in keeping with other studies which have successfully adopted an allometric approach to biomass estimation (Haase and Haase, 1995; Guevara et al., 2001; Mani and Parthasarathy, 2007). This approach allows large areas to be sampled with ease and overcomes issues of conservation concern related to destructive sampleing (Navar et al., 2004) and confounding factors associated with the use of remote sensing for biomass estimation such as topographical variation and radiometric disturbance (Box et al., 1989). The observer bias that might be anticipated given that this method is also based on an extrapolation from a cover estimate is laid to rest here (Catchpole and Wheeler, 1992). In the literature, concern is raised over the use of logarithmic

transformation and the introduction of bias when reverting to original units. However, as logarithmic transformations were used so rarely in this study, this is felt unlikely to affect the overall results (Baskerville, 1972; Soares and Schaeffer-Novelli, 2005).

The use of regression equations based on allometric relationships, with limited destructive sampling, generally proved effective (Flombaum and Sala, 2007). However, the potential to generalise these findings for groups of species not sampled here, proved unsuccessful. This was disappointing given the recent success of Flombaum and Sala (2007) in deriving generalised volume-biomass curves. In this current study the few relationships established were erratic, in no way allowing for generalisations. It would seem species in this area are in fact very specific in their volume to biomass relationship. The regression relationships established here, while unable to be extended to species beyond this study, will contribute to a growing pool of such equations for future use (Milton, 1990a; Flombaum and Sala, 2007). There is also scope to test intraspecific allometric regression relationships, where plants alter allocation patterns in response to edaphic factors, climate, disturbance and age; presenting plasticity across different geographic areas (Milton, 1990b; Northup et al., 2005; Soares and Schaeffer-Novelli, 2005).

6.4.6 Impacts of grazing measured through perennial biomass

This study demonstrates the effective use of linear-regressions based on allometric relationships where reliable values for standing perennial biomass were generated for the vegetation types under consideration. Sustained heavy grazing is shown to significantly reduce biomass on the communal range on the highly accessible sandy lowland areas virtually throughout the Kamiesberg. The loss in biomass is principally of highly palatable species, with no evidence of a response in terms of annual biomass, although the proliferation of annuals on the open ground of communal rangelands is well documented. As an intrinsic response to abiotic and biotic drivers, perennial biomass measured in this study tells us firstly that environmental variability across the Kamiesberg results in highly heterogeneous biomass, and secondly that the sustained heavy grazing associated with the communal rangelands is degrading the lowland areas.

An examination of the potential to group species architecturally and develop generic regression curves for more widespread biomass studies proved unviable. While this demonstrates the unique intraspecific nature of allometric relationships, the somewhat rough nature of biomass assessment is acknowledged. On this basis it is hoped that the regressions generated here, as well as the broader biomass values, may be effectively used in future modelling or comparative exercises.

7. ASSESSMENT OF VEGETATION PATTERNS AND LAND USE IMPACTS USING SPECTRAL INFORMATION DERIVED FROM LANDSAT 7 IMAGERY

Abstract: In this chapter a supervised classification technique is applied to a remotely sensed image from the Landsat 7 EMT+ sensor to generate thematic maps of the study area. Following statistical exploration, three maps were generated, one based on the original multispectral bands, one on plant cover and one on plant biomass based on a Normalised Difference Vegetation Index (NDVI) image. Despite strong correlations between spectral signatures and cover and biomass, the resultant thematic maps do not comply with the generally accepted accuracy assessment standards. It is argued that they still hold considerable value as comparative tools, both with ground-based analyses, and as relative measures against each other. Significant evidence of land-use impacts measured in the field (Chapters 4 and 6) are not evident in this analysis. This is attributed to a number of possible causes including mixed pixels due to the fence-line nature of the ground-truthed data and subsequent close proximity of training sites, weakening the resultant spectral signature. While this study shows potential for future work using remote sensing in the area, it should be used as a complementary tool in conjunction with other datasets rather than a stand-alone tool.

7.1 INTRODUCTION

Earlier chapters show that vegetation types described in this study are discrete in terms of plant species composition and abiotic constituents (see Chapter 3), and that sustained heavy grazing of these vegetation types has resulted in changes in cover, species composition and plant biomass (see Chapters 4, 5 and 6). In this chapter a supervised classification technique was applied to a remotely sensed image from the Landsat 7 EMT+ sensor to generate thematic maps of the study area and surrounds based on field measures. Three approaches were explored: firstly using the original multispectral bands of the Landsat 7 image, secondly using a Normalised Difference Vegetation Index image (NDVI), and thirdly a Modified Soil-Adjusted Vegetation Index (MSAVI). The resultant thematic maps were examined for corroborative evidence of vegetation patterns and land-use impacts measured on the ground.

The restricted nature of the temporal and spatial scale of field data limits its usefulness for detecting and predicting larger scale regional or global vegetation patterns, and in turn any change in vegetation types over time. Satellite imagery is recognised as a vital tool in extrapolating local understandings to greater areas

(Hobbs, 1989; Kerr and Ostrovsky, 2003; Turner et al., 2003; Shupe and March, 2004). The scales at which remote sensing can operate means it is a way of circumventing variable field techniques, the spatial heterogeneity of landscape patterns, and the considerable cost of extensive field surveys (Washington-Allen et al., 2006). This ability to generate thematic maps for large areas with relative efficiency has resulted in more frequent use of remote sensing technology in the generation of vegetation and cover maps for use in a number of areas, one of which is the ecological monitoring of rangelands (Moleele et al., 2001; Archer, 2004; Calvao and Palmeirim, 2004; Washington-Allen et al., 2006). Indeed the large areas under range management and the frequently remote nature of rangelands, in combination with the diversity and intensity of pressures on them, make visual interpretation a valuable management tool (Bark et al., 1999; Saltz et al., 1999; Lillesand and Kiefer, 2000; Wessels et al., 2004). Historically there has been a perception that the scales at which remote sensing and field ecology operate are irreconcilable. However, improved imagery resolution and image processing software, combined with evidence of numerous successful studies are serving to dispel this misconception (Turner et al., 2003). There is a growing view that the objective, systematic, repeatable and spatially explicit nature of remote sensing analysis may make it a highly effective tool in alteration assessment (Wessels et al., 2004), the definition and measurement of which is fraught with controversy (Ash et al., 2001; Reynolds and Stafford Smith, 2001; Gillson and Hoffman, 2007). Remote sensing is described as a powerful new tool available to ecologists and conservation biologists (Kerr and Ostrovsky, 2003).

In southern Africa satellite imagery has been successfully used to explore and map plant communities (Palmer, 1991; Shiponeni, 2007), examine landscape level change (Wessels et al., 2004; Wessels et al., 2007), and on a finer scale to investigate grazing impacts (Archer, 2004). The use of the tool in rangeland science in southern Africa has been described as promising (Archer, 2004). In the immediate study area two localised studies have demonstrated successful correlations between vegetation cover and remote sensed indices (Byers, 2005; Shiponeni, 2007), and another showed the effective use of remote sensing in tracing phenological patterns at the landscape scale (Fox, 2003).

This chapter adopts three different approaches in generating supervised classifications off a Landsat 7 image, and then examines the value of three thematic maps created in the process. More specifically the following questions are addressed:

1. Can findings established from field observations in this study (vegetation patterns and grazing impacts) be detected in a greater geographic area through the development of thematic maps through supervised classification of a Landsat 7 image?

2. Of the three approaches explored in the generation of thematic maps (using the original multispectral bands, an NDVI and an MSAVI image) which, if any, is best suited for expanding ground-truthed data to the greater area?

7.2 METHODS

7.2.1 Field data

Data collected and processed relating to plant community composition, cover and standing perennial biomass were used in this study (see Chapters 3 and 6 respectively for methodological details). Coordinate location points were collected at three of the four corner points of each field site using a Global Positioning System (GPS). Coordinate locations were entered into a Geographic Information System (GIS) as a shapefile using the software package ERDAS Imagine and these were laid over the Landsat 7 image.

7.2.2 Satellite Imagery

Remotely sensed reflectance values were derived using a single Landsat 7 image from August 2000. Landsat 7 is collected in an earth observing instrument called the Enhanced Thematic Mapper Plus (ETM+). In addition to a panchromatic band, the EMT+ collects seven bands of data: six bands in the visible, near infrared and mid-infrared spectrum and a thermal band. On-board radiometric calibration is within an accuracy of 5% and the resultant ground resolution cell size is 30 m x 30 m (Lillesand and Kiefer, 2000).

Vegetation has high near-infrared reflectance and low visible reflectance as a result of scattering in the mesophyll, and visible-wavelength absorption through pigments such as chlorophyll. On this basis vegetation indices are used to generate a parameter that is correlated with the amount of vegetation present in a pixel (Rees, 1999). This study used two indices, the Normalised Difference Vegetation Index (NDVI) and Mean Soil Adjusted Vegetation Index (MSAVI). NDVI has been successfully used in vegetation mapping exercises and in examining vegetation dynamics (Saltz et al., 1999; Weiss et al., 2004; Pettorelli et al., 2005; Barbosa et al., 2006), and is favoured as it compensates for extraneous factors such as changing illumination conditions and surface slope (Lillesand and Kiefer, 2000). The MSAVI takes into account the effect of bare soil between plants on the ground and was developed in an attempt to address problems arising from high soil reflectance, particularly in arid areas where cover is less than 25% and soil reflectance high (Qi et al., 1994; Rondeaux et al., 1996).

7.2.3 Biomass and cover correlations with NDVI and MSAVI

Field sites were used to generate training sites for the creation of reflectance signatures. Three sets of signatures were generated;

- (A) one from the original multispectral bands of the Landsat 7 image,
- (B) a second from a Normalised Difference Vegetation Index (NDVI) image, and
- (C) the third off a Modified Soil-Adjusted Vegetation Index (MSAVI).

The NDVI and MSAVI were computed from reflectance values using the following equations respectively:

$$NDVI = (r_{NIR} - r_{RED})/(r_{NIR} + r_{RED}) \quad (1)$$

$$MSAVI = [(r_{NIR} - r_{RED})/(r_{NIR} + r_{RED})] * (1+L) \quad (2)$$

where r_{NIR} and r_{RED} are reflectance in the near-infrared and red bands, and L is a soil adjustment factor derived using the product of the NDVI and a weighted difference vegetation index (Qi et al., 1994). The cloud free image in the standard projection Universal Transverse Mercator (UTM) with the spheroid and geodetic datum WGS 84

was geometrically corrected by the German Aerospace Centre (DLR)´s Remote Sensing Data Center (DFD) prior to analysis. Root mean square error (RMSE) after the geometric correction was lower than half the pixel size, i.e. < 15 m. The NDVI image was generated by the author and the MSAVI image by BIOTA staff at the DFD.

The relationship between reflectance signatures for all three images and ground-truthed data were explored in STATISTICA using regression analysis.

To test whether differences in field data attributable to variable grazing intensity (see Chapters 4 and 6) could be detected in the remotely sensed image a single factor analysis of variance (ANOVA) for parametric data was used to test for significant differences in the spectral signal of the two indices for private and communal rangelands across the entire study area. In examining NDVI spectral differences between communal and private rangelands in each vegetation type, data were non-normal. In this case a Kruskal-Wallis ANOVA and median test for non-parametric data was used to test for significant differences.

7.2.4 Supervised classifications

Three supervised classifications, based on the Landsat 7 image were carried out using the Erdas IMAGINE software. In supervised classification, information derived from field studies at known locations are used to generate training sites. The region growing seed pixel method uses a selected target seed (the original field site), analyses the spectral properties of the pixels and uses these to merge immediately adjacent like-pixels into a larger homogenous training site. Merge tolerance, which specifies the Euclidean distance in feature space, was set to 10. These training sites are used by the software to group pixels of the same spectral response. The result is a thematic map where spectrally similar pixels are attributed the same ground-truthed values (Rees, 1999). With a minimum of three pixels per training site, a total of 198 training samples were used. These were split between six classes, reducing the number of signatures for each class. The (A) first classification was generated using the Erdas IMAGINE supervised classification routine where geolocated ground-truthed information was used to extract characteristic spectral signatures from the spectral Landsat 7 image stack. The respective signatures were used to train the

supervised, maximum likelihood, classification. Following initially very low accuracy assessments (see later for method details) a combination of visual assessment (where classes where excessively mingled) and prior knowledge (emerging from the vegetation characterisation, see Chapter 3), were used to regroup certain classes. Resultant thematic maps were assessed for an improved accuracy assessment value.

The second two classifications were conducted on the basis of the significance of relationships found between the NDVI signal (B) and cover and biomass. As the MSAVI signals (C) did not correlate significantly with the biomass measures no further analysis was carried out on this image. Using histograms of the cover and biomass values, NDVI spectral response and associated cover and biomass classes were created. These in turn were used to generate classifications, using the Erdas IMAGINE classification tool, where pixels were grouped according to their reflectance signature, and correlated cover or biomass class.

An accuracy assessment was carried out on each thematic map using the ERDAS Imagine Accuracy Assessment tool. GPS points and associated cover values collected prior to the initial field work season in June 2002 were used for this purpose. In the accuracy assessment the value of each of these points was compared to the value attributed to that site in the supervised classification. On this basis an error matrix was generated. The error matrix reported four statistics: producer's accuracy, users'accuracy, overall accuracy and a Kappa statistic (Stehman and Czaplewski, 1998). The producer's accuracy gives the number of correctly classified pixels out of the total number of reference pixels in a class, demonstrating how well the original training pixels were classified. The user's accuracy gives the number of correctly classified pixels per class, showing the probability of a classified pixel actually representing that category in reality. Overall accuracy is the percentage of correctly classified reference pixels and the Kappa statistic gives an overall classification accuracy taking variation in class size into account.

7.3 RESULTS

7.3.1 Plant cover and biomass correlations with remote sensing derived indices

Regression analysis of percentage plant cover recorded for the 66 field sites and NDVI showed a significant relationship ($r^2 = 0.371$, $p < 0.001$). A similarly significant relationship was found between biomass and NDVI ($r^2 = 0.343$, $p < 0.001$) (Figures 7.1 and 7.2). While a significant relationship was also evident between percentage plant cover and the MSAVI signal ($r^2 = 0.472$, $p < 0.001$), no similar significant relationship was found between the MSAVI signal and biomass ($r^2 = 0.01$, $p > 0.1$). In light of this only the NDVI-derived images were used in generating thematic maps of the area.

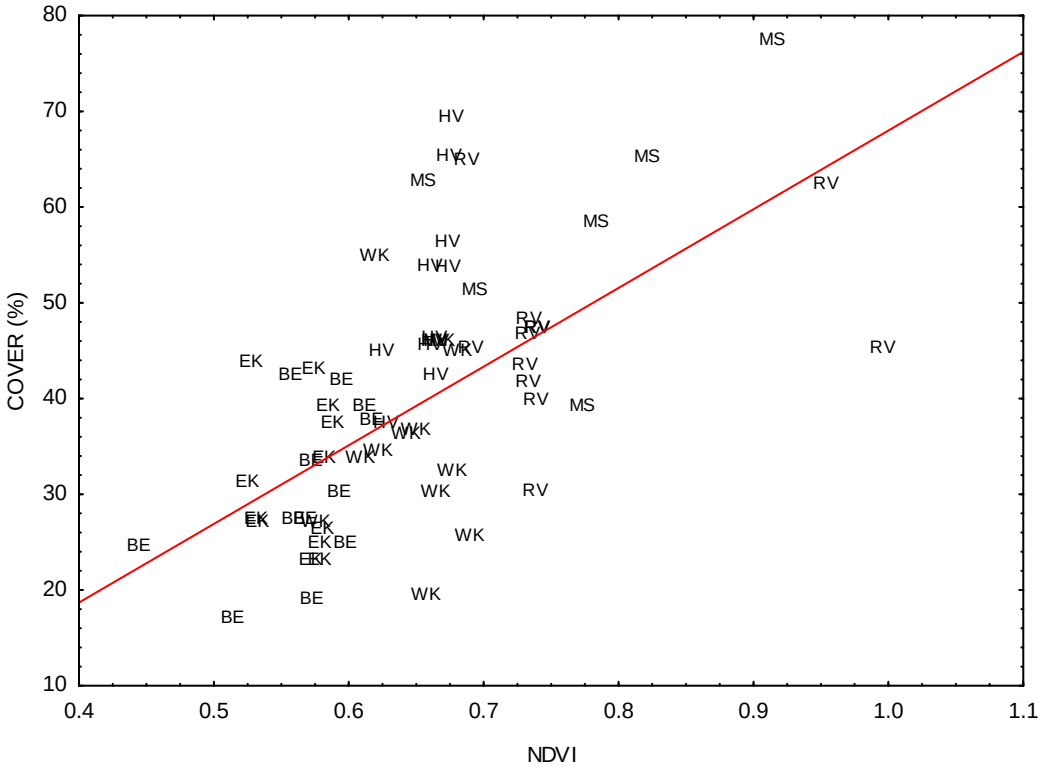


Figure 7.1 Regression analysis for plant cover and NDVI reflectance values for the 66 sites sampled in six vegetation types across the Kamiesberg Mountain range (HV = Heuweltjieveld, WK = Western klipkoppe, MS = Mountain shrubland, RV = Renosterveld, EK = Eastern klipkoppe, BE = Bushmanland ecotone).

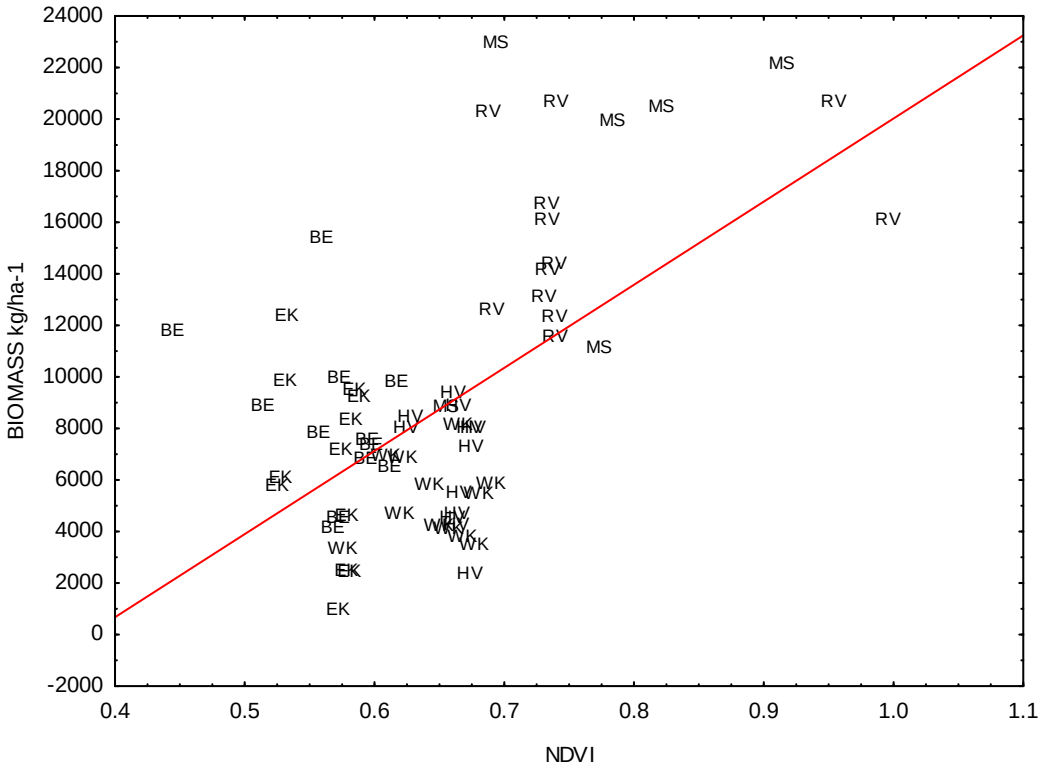


Figure 7.2 Regression analysis for standing perennial biomass and NDVI reflectance values for the 66 sites sampled in six vegetation types across the Kamiesberg Mountain range (HV = Heuweltjieveld, WK = Western klipkoppe, MS = Mountain shrubland, RV = Renosterveld, EK = Eastern klipkoppe, BE = Bushmanland ecotone).

7.3.2 Maps generated on the basis of field data and established relationships

Three thematic maps of the Leliefontein area and surrounds were successfully generated. The first (Figure 7.3) is based on the original multispectral bands of the Landsat 7 image (A) and appears to reflect the difference in vegetation to the west and east of the Kamiesberg, with Eastern klipkoppe lowlands in light blue to the east and the Western Klipkoppe and Heuweltjieveld lowlands in orange to the west. Klipkoppe vegetation rings the Kamiesberg in the mid-altitudes in dark blue and the Renosterveld and Mountain shrubland vegetation types are evident at the higher, central regions of the Kamiesberg in purples and darker green respectively.

The second thematic map (Figure 7.4) is a cover map based on the NDVI (B) signature. Visually this distinguishes the higher altitude regions at the centre of the map as having high cover in reds and darker greens, with reduced cover to the west in white and lighter pinks. While cover does not vary significantly between the Western

and Eastern klipkoppe vegetation types (see Chapter 3), apparent differences here must be attributed to the composition of the cover in question, where these vegetation types have been shown to be compositionally distinct. The third thematic map (Figure 7.5) is a biomass map also based on the NDVI signature. Visually this shows the considerably greater biomass in the higher altitude regions at the centre of the Kamiesberg in purples and the higher biomass associated with the western slopes associated with higher rainfall, in dark green. Lower biomass is evident to the east in light pink and light green.

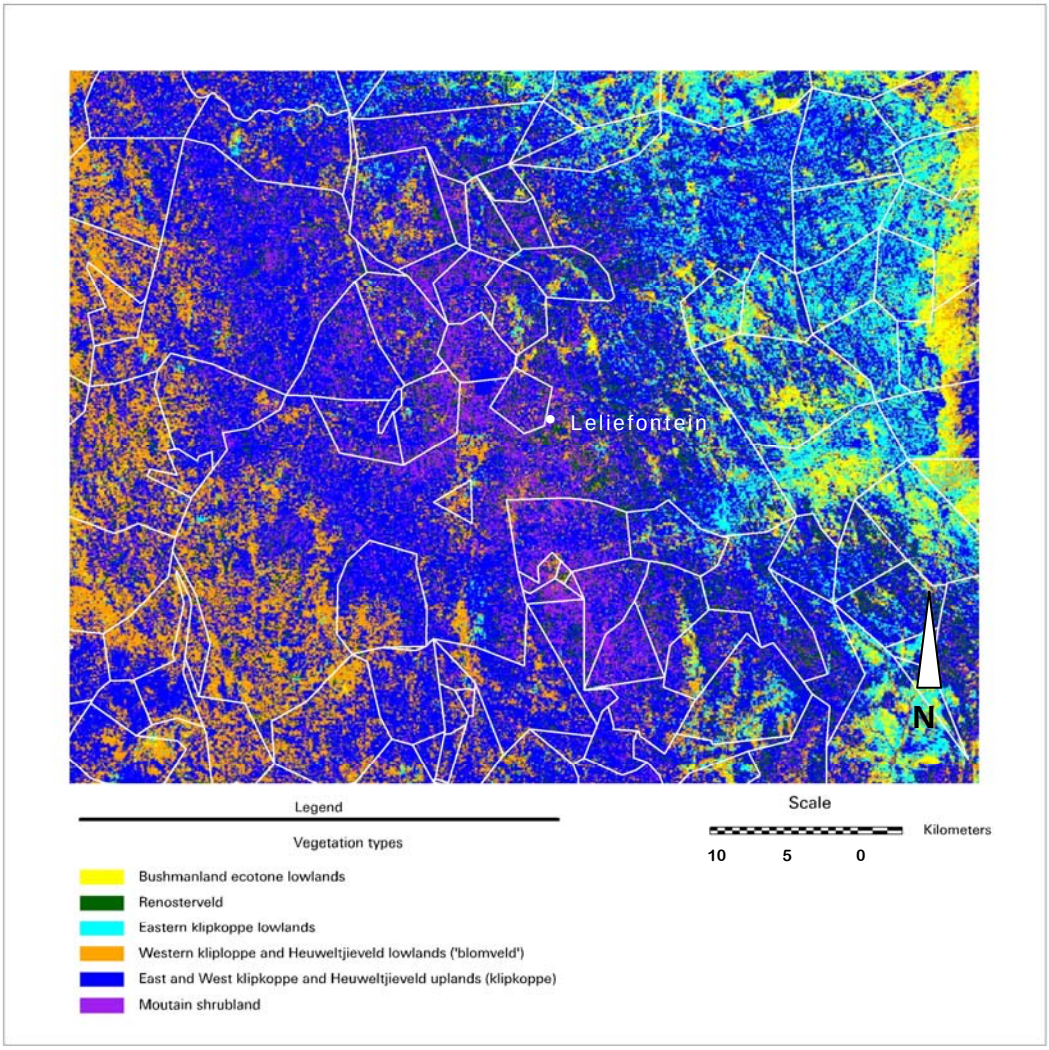


Figure 7.3 Supervised classification, based on spectral Landsat 7 bands, of the vegetation of the Kamiesberg and surrounds. White lines indicate cadastral boundaries. The large area in the centre of the image is the Leliefontein communal area.

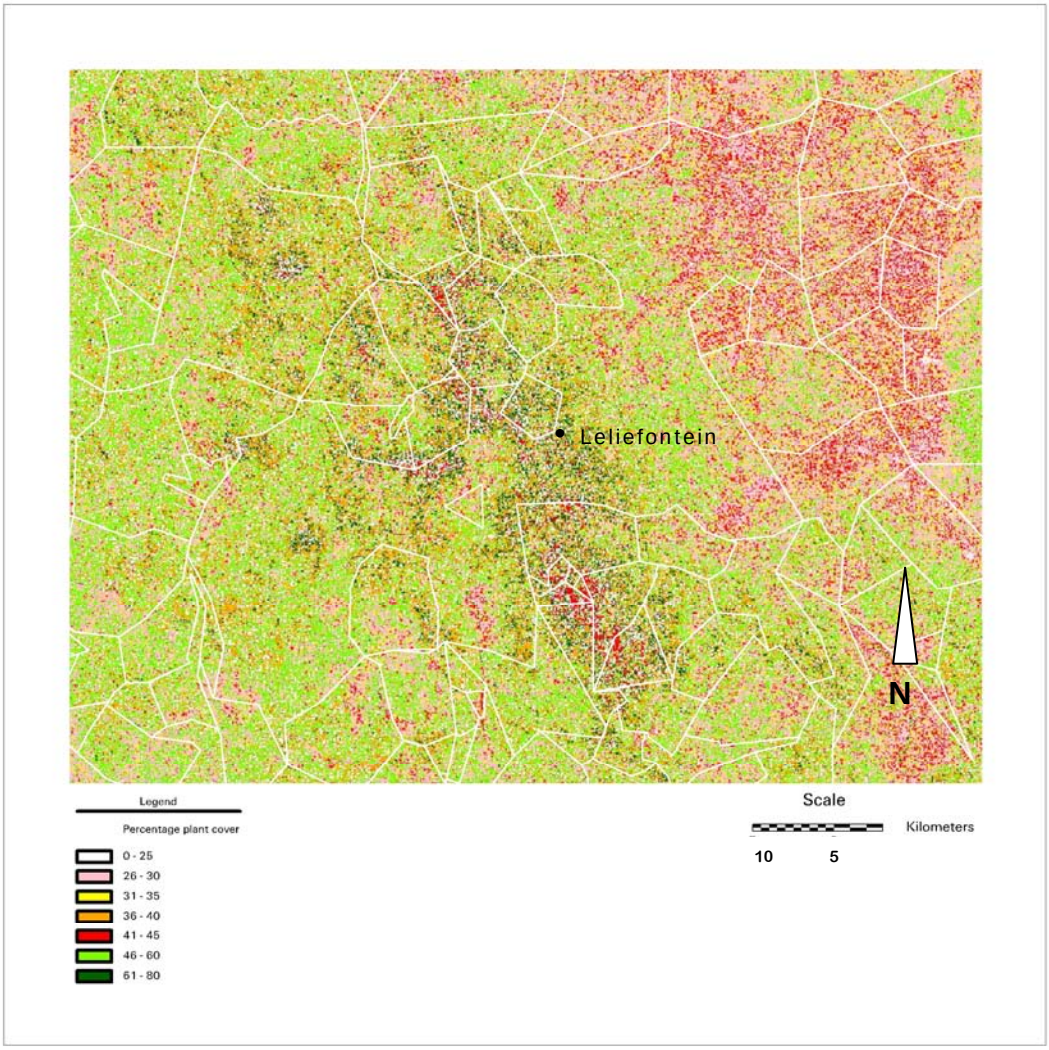


Figure 7.4 Supervised classification of plant cover, based on NDVI, of the vegetation of the Kamiesberg and surrounds. White lines indicate cadastral boundaries. The large area in the centre of the image is the Leliefontein communal area.

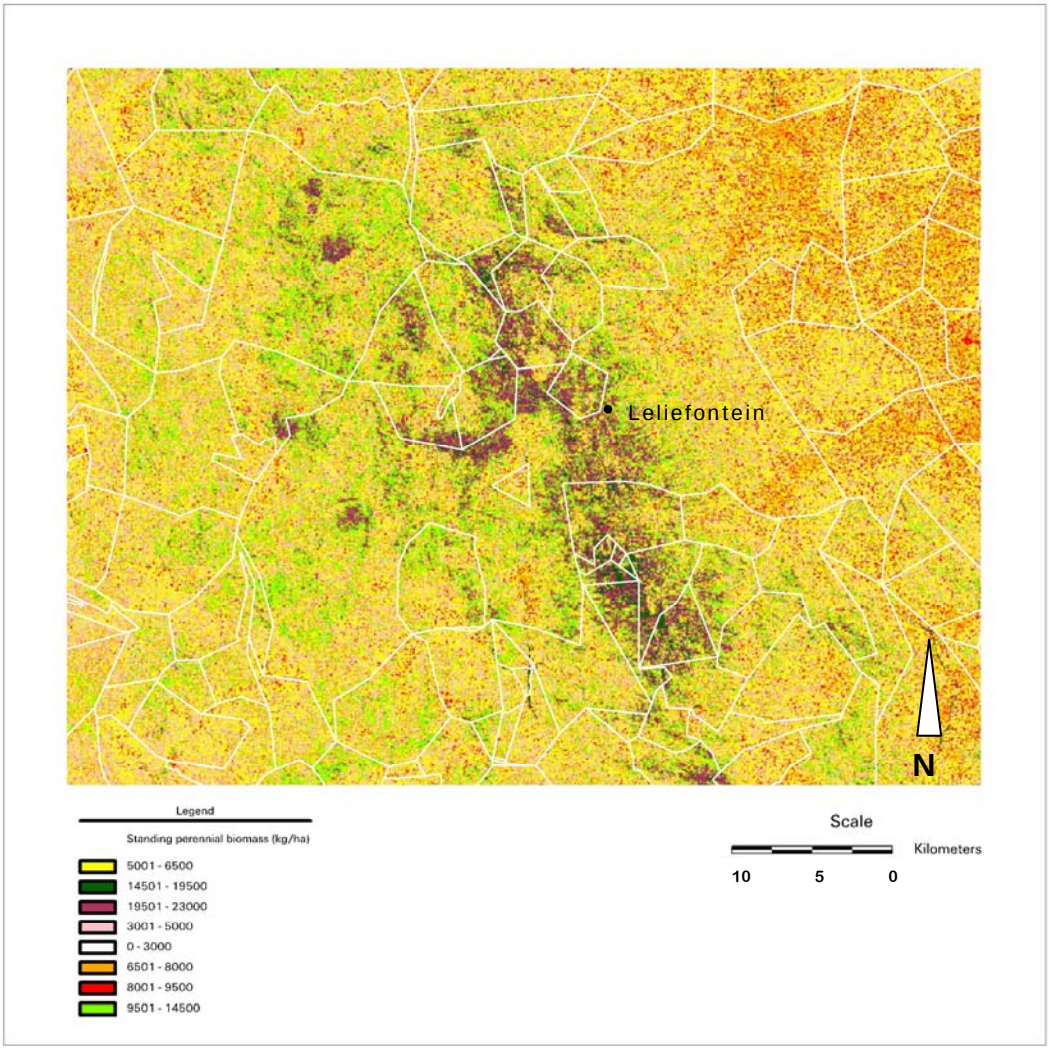


Figure 7.5 Supervised classification of standing perennial plant biomass, based on NDVI, of the Kamiesberg and surrounds. White lines indicate cadastral boundaries. The large area in the centre of the image is the Leliefontein communal area.

7.3.3 The detection of land-use response in satellite imagery

The single factor analysis of variance (ANOVA) showed that the NDVI and MSAVI spectral responses did not differ significantly across all vegetation types in the study site as a function of land use. Similarly, no significant differences were found between communal and private rangelands within each vegetation type.

7.3.4 Thematic map accuracy assessment

The accuracy assessment of the thematic map generated off the multispectral band image (A, Table 7.1) and the NDVI-based cover classification (B, Table 7.2) showed the classifications to be low in overall accuracy although some classifications were better than others. Notable are the user's accuracy of the multispectral band image for classes 2 and 3 where accuracy is 100% and 82% respectively. Misclassifications between vegetation types were most common among classes 4 and 5, representing the Western klipkoppe and Heuweltjieveld lowlands, and Eastern and Western klipkoppe uplands respectively. Misclassifications between cover classes were generally to an adjacent class with the exception of class 4, where misclassifications were spread among a number of classes. No accuracy assessment was possible for the NDVI-based biomass classification as test points collected in June 2002 did not includ a detailed biomass assessment.

Table 7.1 Error matrix of the classification of the Landsat 7 image based on vegetation type. Class categories are as follows: Class 1 = Bushmanland ecotone lowlands, Class 2 = Eastern Klipkoppe lowlands, Class 3 = Renosterveld, Class 4 = Western klipkoppe and Heuweltjieveld lowlands, Class 5 = Eastern and Western klipkoppe uplands, Class 6 = Mountain shrubland.

	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Classified total	User's accuracy
Class 1	4	1	0	0	1	0	6	67%
Class 2	0	1	0	0	0	0	1	100%
Class 3	1	1	9	0	0	0	11	82%
Class 4	3	3	2	10	2	0	20	50%
Class 5	4	7	3	2	15	0	31	48%
Class 6	0	0	0	0	0	0	0	-
Referenced totals	12	13	14	12	18	0	69	
Producer's accuracy	33%	8%	64%	83%	83%	-		
					Overall classification accuracy			56%
					Overall Kappa (k) statistics			0.44

Table 7.2 Error matrix of the classification of the Landsat 7 image and thematic map based on plant cover. Class values are as follows: Class 1 = 0 – 25%, Class 2 = 26 – 30%, Class 3 = 31 – 35%, Class 4 = 35 – 40%, Class 5 = 41 – 45% , Class 6 = 46 – 60%.

	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Classified total	User's accuracy
Class 1	15	6	1	0	0	0	22	68%
Class 2	0	6	4	0	1	0	11	55%
Class 3	1	0	10	4	1	0	16	62%
Class 4	2	1	5	12	2	0	22	54%
Class 5	2	0	0	0	5	0	7	71%
Class 6	0	0	0	0	1	2	3	66%
Referenced totals	20	13	20	16	10	2	81	
Producer's accuracy	75%	46%	50%	75%	56%	100%		
					Overall classification accuracy			62%
					Overall Kappa (k) statistics			0.52

7.4 DISCUSSION

7.4.1 Thematic map accuracy considerations

The thematic maps generated did not achieve the commonly recommended overall accuracy target of 85% (Foody, 2002). This failure to meet accuracy requirements is described as a frequent problem, attributed to issues such as complex assumptions, sampling design and the accuracy of ground-truthed reference data (Foody, 2002; Fassnacht et al., 2006). Indeed in their assessment of the effective use of remote sensing, Fassnacht et al. (2006) describe maps derived from remote sensing as commonly inaccurate. As the value of each thematic map is assessed, possible confounding factors accounting for the low accuracy measures are considered.

7.4.2 Maximum likelihood derived vegetation map of the Kamiesberg and surrounds

The vegetation map (A) that gave the highest degree of accuracy was the one that recognised the Klipkoppe uplands as one vegetation type, with no division between the eastern and western components, and the inclusion of the Bushmanland ecotone uplands to the east and the Heuweltjieveld uplands to the west (see Figure 7.3). This

grouping of vegetation types is in keeping with Mucina and Rutherford's (2006) vegetation map for South Africa, for the vegetation type they call Namaqualand Klipkoppe Shrubland. However, an ordination of the field sites on the basis of species composition (see Chapter 4), shows the eastern and western elements as compositionally unique. The high volume of misclassified pixels in classes 4 and 5, representing the Western klipkoppe and Heuweltjieveld lowlands and the Western klipkoppe and Eastern klipkoppe uplands respectively, supports a more refined division of these vegetation types. In the same ordination (see Chapter 4) the Bushmanland ecotone uplands tend to cluster towards the Eastern and Western Klipkoppe in some support of the vegetation map derived here. A western and eastern aspect did come out in the lowland areas of the Klipkoppe vegetation. The Western Klipkoppe lowlands and Heuweltjieveld lowlands made an obvious grouping, in keeping with Mucina and Rutherford's Namaqualand Blomveld vegetation type for the same area (Mucina and Rutherford, 2006). In keeping with the previously mentioned ordination, but in contrast to Mucina and Rutherford's map (where this vegetation is included in the Namaqualand Blomveld), is the independent recognition of the Eastern Klipkoppe lowlands.

While the classification of Mountain shrubland and Renosterveld vegetation types presents no conflict with those of Mucina and Rutherford (2006), the areas covered by these vegetation types appear to vary. Considerably greater area in this classification is recognised as Mountain Shrubland while the inverse is true of Renosterveld. In this current classification in this thesis this is possibly a function of the highly varied nature of those Mountain Shrubland sites that were sampled. In the compositional ordination (see Chapter 4) this vegetation type is the most disparate with some sites apparently clustering closer to the Renosterveld, some to the Heuweltjieveld upland and some to the Western Klipkoppe upland sites. Consideration of the compositional ordination in relation to the spectrally derived vegetation map demonstrates the limitations of a remote sensing approach where spectrally similar, but compositionally unique vegetation types may be incorrectly grouped. This points to the value of using a suite of tools in generating land cover maps (Lillesand and Kiefer, 2000; Fassnacht et al., 2006).

In all instances the boundaries produced in this study were divergent to those of Mucina and Rutherford (2006). With respect to the Mucina and Rutherford map, this may be attributed to the enormity of the area their map covers, as it includes the whole of South Africa, Lesotho and Swaziland, and therefore operates at a less refined scale. The vegetation boundaries in their map for the Kamiesberg area are noted elsewhere as potentially problematic (Desmet and Helme, 2006). In this study however, variable boundaries may be attributable to the difference in years between the image (taken in 2000) and that of field sampling (2002). While rainfall recorded at one site in the study area in Paulshoek to the east of the Kamiesberg, shows the rainfall to be similar for the two years in question (±155 mm for 2000 and ±135 mm for 2002) (Hoffman unpublished data), it is possible that any variation in the seasonality of this rainfall could account for differences. This would also be a factor in the accuracy assessment, where points used in the accuracy assessment were collected prior to the rainy season in the June of 2002. In her remote sensing assessment of phenological responses across Namaqualand, Fox (2003) notes that each vegetation type has its own unique phenological signature, suggesting that the signal produced by these vegetation types could vary significantly with their response to spatially and temporally variable rainfall. While the vegetation types of the Kamiesberg are largely discrete (see Chapter 3), the vegetation, in particular at the boundaries is mosaic-like in nature and there is the chance that a commonly recorded problem of mixed pixels in the training sites could have weakened the resultant thematic maps (Pettorelli et al., 2005). One over-view of remote sensing techniques suggests the value of a continuous rather than a class-based approach to classification. In the Kamiesberg where vegetation boundaries are unclear this may be a better approach to adopt in future studies (Fassnacht et al., 2006). The patchy nature of the map generated in this study is probably reflective of both the mosaic-like nature of the vegetation of the Kamiesberg and the fact that the map needs further verification across a greater area and subsequent simplification. There is scope for further comparative work examining these classifications in relation to other mapping work being carried out in the region (Desmet and Helme, 2006), particularly in light of conservation initiatives currently underway in the area.

7.4.3 Plant cover and biomass correlations with vegetation indices

The significant correlations generated between plant cover and biomass and NDVI in this study are in keeping with previous and well demonstrated studies that show that a Landsat 7 image can be effectively used to expand the findings of a localised study to a greater landscape scale (du Plessis, 1999; Lillesand and Kiefer, 2000; Langley, 2001; Shiponeni, 2007). Indeed when assessed visually in the context of a detailed understanding of the area as generated in the vegetation characterisation (Chapter 3) the derived maps appear to support these significant relationships and have worth in excess of that reflected by the accuracy assessments. It is likely that a greater number of training sites, particularly given the heterogeneous nature of the vegetation in the study area, would strengthen the correlations. That this did not translate into a rigorously accurate thematic map is attributed to the fact that the accuracy assessment points were both taken at a different time of year, before the effects of the wet season had registered which would have dramatic effects on the plant cover.

A question is raised regarding the discrepancy in the relationship between biomass and the NDVI, and biomass and the MSAVI. The choice to use MSAVI as one of the indices to be explored was based on a successful correlation with plant cover established in previous work in a smaller-scale study in the Paulshoek area (Byers, 2005). Furthermore, the MSAVI was developed in an attempt to address the high soil reflectance problems associated with arid environments where cover is less than 25% and soil reflectance high (Qi et al., 1994; Rondeaux et al., 1996). Given this, the failure to correlate standing biomass and MSAVI was surprising. The literature shows a relatively early interest in the use of remote sensing to estimate standing dry biomass, and simultaneously records a number of problems in relating biomass and reflectance (Ringrose et al., 1989; Moleele et al., 2001; Hunt et al., 2003; Calvao and Palmeirim, 2004). In this study the highest biomass values recorded, which were in the Mountain Shrubland and Renosterveld vegetation types, are associated with the greatest rock cover as they grow at the top of the Kamiesberg Mountain and it is possible that the soil adjustment factor associated with the MSAVI combined with the particular reflectance value of the rock, where mountains are known to produce spectral 'noise', confound the relationship. Both rock cover and bare ground are often associated with lichens and other biological crusts. This is a contributing factor not recorded in this study, but certainly one that would also vary between seasons and

years. This could present spectral responses out of keeping with values recorded as bare ground or bare rock in the cover data collection process in the field (Solheim et al., 2000; Orlovsky et al., 2004).

7.4.4. The value and potential use of the vegetation index derived classifications

While the overall accuracy of the cover map is lower than the multispectral supervised maximum likelihood classification and subsequent vegetation map, the two thematic maps generated of vegetation cover and biomass both have their merits and are worthy of discussion. The thematic map based on cover reflects the high rock cover across the top of the Kamiesberg Mountains, evident in patches of white and light pink indicating very low cover. This is not apparent on the biomass classification which simply attributes high biomass, indicated by dark green and maroon, to this area. Once again this may be attributable to a spectral response from lichens. In this instance these maps are best viewed in conjunction, where an understanding of a combination of low cover and high biomass can be indicative of the rocky upland areas of the Kamiesberg (see Chapters 3 and 6). The biomass classification picks up on the high biomass associated with river systems, and these are more readily visible on this classification. In the Heuweltjieveld there is generally high cover, but moderate biomass, demonstrating that one cannot simply assume that cover translates to biomass. If climate change occurs as predicted (MacKellar et al., 2007), snap-shot views of vegetation, related to current ground-truthed data, and verified, will become important datasets for temporal comparison or future modelling exercises (Hobbs, 1989) and useful tools for monitoring extensive rangelands (Washington-Allen et al., 2006). However, it is likely that more readily comparable hypertemporal datasets such MODIS will have a more significant role in such assessments.

Neither classification produced any visible evidence of the frequent fence-line contrasts of the area. This is supported by the lack of any significant differences in spectral response in the original signatures on the basis of land-use. The nature of this current study, based as it was on fence-line contrast sites where training sites are in close proximity to one another, may have given rise to a greater number of mixed-pixels (Pettorelli et al., 2005), confounding the extrapolation of the ground-truthed evidence of land-use impacts. In their study of grazing impacts in the Negev desert in Israel, Saltz et al. (1999) also failed to detect ground-truthed grazing impacts in a

detailed remote sensing analysis. They attribute this to the low vegetation cover of arid areas where a loss of 30% cover or biomass to heavy grazing may in fact reflect a shift from 15.8% cover to 11.2% cover, which translates to a mere 4% loss of total cover (Saltz et al., 1999). However, some remote sensing studies have successfully demonstrated land-use impacts and what they term degradation (Barbosa et al., 2006), including a study of other communal areas, though situated in a more mesic environment, in South Africa (Wessels et al., 2004), and one in the arid eastern Karoo in South Africa (Archer, 2004). Arid lands are noted as potentially problematic, and one study suggests more detailed data processing with attention to outliers may resolve some of the issues associated with low vegetation cover (du Plessis, 1999). These more successful studies, in combination with the strong correlations between NDVI and cover and biomass, and the overall accuracy assessment of this study points to the potential for a more refined approach. On this basis it is suggested that the exploration of land use impacts through remote sensing still remains a possibility in this area.

Consideration of the vegetation classification and the cover and biomass classifications, points to the coarse nature of this remote sensing analysis. This is likely to be a function of both the resolution of the Landsat 7 image which operates at a 30 m x 30 m scale, the heterogeneous nature of the vegetation of the area (Bark et al., 1999), and the relatively limited number of training sites across a large and heterogeneous area. A further consideration is the much localized area used in determing cover on the ground. These factors might lead to a situation where there are spectrally mixed pixels and thus an unlimited possibility of spectral classification of single classes, especially when spatial patchiness of the landscape is near or below the spatial resolution of the imagery. Additional considerations likely to elucidate changes in rangeland condition are a more extensive temporal scale and the use of a more telling index such as Rain Use Efficiency, which has been effectively used elsewhere in examining rangeland dynamics (Wessels et al., 2007).

The exploration of spectral signatures and vegetation types in the original multispectral Landsat 7 image demonstrated that without a detailed understanding of the vegetation types on the ground, there is potential to oversimplify vegetation patterns. All the analyses served to demonstrated that to produce accurate thematic

maps using supervised maximum likelihood classifications and regression analyses rigorous consideration needs to go into the planning of the ground-truthing methodology and the compatibility of the imagery chosen for analysis. However, while the thematic maps generated in this study did not comply with the generally accepted accuracy assessment standards, they still held considerable value as comparative tools, both with ground-based analyses such as the vegetation characterisation, and against each other, highlighting, for example, differences in cover and biomass relationships between vegetation types. This study would therefore agree with Lillesand et al. (2000) who make the point that Landsat should be used as a complementary interpretive tool, in conjunction with other datasets, and not as a stand-alone tool.

8. CONCLUSIONS

This study set out to establish whether the sustained heavy grazing associated with the Leliefontein communal rangeland, situated in arid Namaqualand, impacts on the vegetation of the area. This was done first by developing a detailed understanding of the vegetation of the area, and then through the systematic examination of the effects of sustained heavy grazing on the vegetation. The research was carried out against the background of the debates in the literature around rangeland ecological theory, the notion of alteration, conservation and ecosystem functioning, and the challenges of measuring change. This chapter considers the findings established in the course of this study, based once again in the broader context of the literature. Finally, consideration is given to recommendations arising out of this work and of possible future research directions.

8.1 CHARACTERISING THE VEGETATION OF THE KAMIESBERG

8.1.1 Understanding system drivers

The characterisation and descriptive analysis of the sites sampled in this study broadly suggests three ecoregions. A western ecoregion which is relatively more climatically moderate with fine, sodium-rich soils, an upper ecoregion of higher rainfall, cooler seasonal temperatures with a high number of frost days and high rock cover, and an eastern ecoregion which is characterised by low and predominantly summer rainfall, seasonally extreme temperatures and coarse, deep soils. A gradient in vegetation echoes this, with a high degree of succulence in the western ecoregion, greater cover and larger woody shrubs in the upper ecoregion and the intrusion of grass in the western ecoregion. This analysis provides a detailed description of the vegetation types in which sample sites were situated. These sites were based on the recent map of Mucina and Rutherford (2006) with some refinement by the author and site details contribute to our understanding of the ecology of the Kamiesberg. At the western extreme the Heuweltjieveld has highly saline, deep soils and is dominated by succulent species, while the Western klipkoppe has shallow soils with greater rock cover and is characterised by a mix of succulents and

dwarf shrubs. On the western slopes of the Kamiesberg is the Mountain shrubland which has little rock cover, with deep acid soils and is dominated by taller shrubs and the few trees that grow in this area. At the top of the mountain is the Renosterveld which receives the highest rainfall and is characterised by the Renosterbos, *Elytroppapus rhinocerotus* and other woody shrubs with some grass cover. The Eastern klipkoppe has a similar substrate to the Renosterveld but is considerably more xeric with lower plant cover of a mix of woody shrubs and succulents. At the eastern extreme the Bushmanland ecotone has coarse, deep soils and is dominated by the grass *Stipagrostis brevifolia*. What emerges is a complex system where climatic and soil variables give rise to a heterogeneous landscape, over which the topographical mask of sandy lowland and rocky upland habitats further contributes to landscape diversity. Each vegetation type is dominated by its own suite of species, with few species ubiquitous to the whole area. This turnover in species composition underscores the high botanical diversity recorded by many other researchers working in this region (Hilton-Taylor, 1996; LeRoux, 2005). Consideration of environmental change in the context of this heterogeneous landscape, with its diverse vegetation types, demonstrates the difficulties of making predications as to how the vegetation types will respond to climate change. The subtleties of abiotic drivers in combination with inferred and cited competitive dynamics, and the demonstrated diversity in individual species' responses make apparent an intricate ecological system.

8.1.2 Providing a benchmark for future work

The insight gained through the detailed description of the sample sites contributes to the important task of providing a detailed characterisation of the Kamiesberg region. The literature calls for thorough ecological studies in generating reference points against which change can be measured (Birch et al., 1999; Fernandez et al., 2001; Veron et al., 2006). The Kamiesberg serves combined roles, firstly as a significant contributor to the status of the broader area as one of only two biodiversity hotspots in an arid region (Hilton-Taylor, 1996; Mittermeier et al., 2004), and secondly as home and a source of livelihood to communal farmers. Indeed just as there are calls for its inclusion in a formal conservation plan (Helme, 1992; Desmet, 1999; Lombard et al., 1999; Desmet and

Helme, 2006), there is an acknowledged need to improve the livelihoods of the communal farmers living in the area (Rohde et al., 2006). The establishment of an understanding of the current status of the vegetation types and ecology of the area is vital to inform future studies, and policy and management decisions for this area.

8.2 GRAZING IMPACTS IN THE KAMIESBERG IN THE CONTEXT OF THE LITERATURE

8.2.1 Rangeland alteration

While the term degradation is still debated (Ash et al., 2001; Reynolds and Stafford Smith, 2001; Gillson and Hoffman, 2007), it must also be acknowledged that numerous practitioners recognize some arid systems as being degraded. In terms of the United Nations (UN) Convention to Combat Desertification definition of land degradation which is defined as, '…the reduction or loss of biological and economic productivity…' and later in the same definition details this loss in terms of, 'native perennial plants (cover and biomass)…' (Reynolds and Stafford Smith, 2001), then based on the findings of this study, the Leliefontein communal area must be described as altered. In light of the complexity of the debate around defining degradation (see Chatper 1), while this study makes findings in close support of the UN definition outlined above, the author chooses to adopt a more cautious approach and preferentially uses the term 'alteration'. This study records a total loss of more than 10% of plant cover on the communal lowlands, and a 6% loss in woody perennial shrubs in the same area. With a total cover of only 44.5% on the private lowlands, this 10% loss in plant cover reflects a 25% difference in cover between these treatments. Similarly the 6% loss of woody shrubs, with a total cover of 16%, reflects a 30% difference in woody cover between the private and communal rangeland. There is an associated increase in herbaceous species, with nearly twice as much cover of this seasonally variable component on the communal rangelands, as reflected in a close to 50% shift in the dwarf shrub category which is comprised of short shrubs and herbaceous species, than the adjacent private rangelands (Chapter 4). These findings are supported by the results of the biomass study which shows standing perennial biomass of highly

palatable species on the communal lowlands to be in the region of a quarter of that of the adjacent private lowlands (Chapter 6). This loss in biomass is predominantly in highly palatable species. The plant functional type analysis demonstrates a biogeographic shift, with the intrusion of a characteristically more xeric vegetation type dominated by succulents into the previously more mesic Renosterveld vegetation type (Chapter 5). These findings all point to an altered system. The results of this study are in keeping with numerous grazing studies across the world where systems are described as degraded in light of altered plant community composition and a shift to more 'pulsed' vegetation dynamics tied closely to seasonal rainfall (Hoffman and Cowling, 1990; Beeskow et al., 1995; Martens et al., 1996; Evans et al., 1997; Vetter, 2003).

8.2.2. Grazing impacts and debates in the literature

In terms of the equilibrium versus non-equilibrium debates, on the basis of the high coefficient of variation (CV) of rainfall, which is above the suggested 33%, this study area should best fit a non-equilibrium model (Ellis et al., 1993; Vetter, 2005). At the very least this should be the case at the western and eastern extremes where the CV of rainfall is highest. In this case, based on the non-equilibrium theory there should be no evidence of long-term grazing impacts on the vegetation, where rainfall should drive vegetation condition and not animal numbers (Ellis and Swift, 1988; Scoones, 1995; Vetter, 2005; Campbell et al., 2006; Gillson and Hoffman, 2007). However, an investigation of differences across fence-lines which separate different farming systems and stocking rates suggest that grazing has a significant impact on plant community composition, cover (Chapter 4), biomass (Chapter 6) and biogeographic distributions (Chapter 5) across the majority of the vegetation types covered in this study.

Increasingly it is acknowledged that no system is in an entirely stable state of equilibrium (Hoffman, 1988; Walker, 1993; Cowling, 2000; Reynolds et al., 2007; Richardson et al., 2007), and the findings of this work are therefore not captured by either end of the equilibrium or non-equilibrium continuum (Wiens, 1984). The author would, along with others, argue in favour of disbanding the equilibrium versus non-equilibrium paradigm

when considering rangeland ecology. We are reminded of the dangers of perpetuating conservative and previously challenged discourses (Benjaminsen et al., 2006), and this is never more true than in the case of the equilibrium and non-equilibrium debate, where these two 'camps' have become misguidedly simplistic caricatures of a multitude of subtle and nuanced scientific studies.

This study shows clear density-dependence impacts. It also demonstrates the complexity of the heterogeneous landscape over which land use is imposed. While not directly engaging with social issues, this study acknowledges the significance and diversity of social issues. Given all these factors, where rangelands are intricate social-ecological systems (Walker et al., 2004), the findings of this study would support an argument in favour of a more comprehensive model in addressing rangeland ecology, such as that of Richardson et al.'s (2007) complex dynamics, or Gillson and Hoffman's use of systems theory and 'moving attractors' (2007), which better accommodate the subtle nuances and complexities of individual rangelands. This study demonstrates the importance of detailed ecological field measures in elucidating ecological change and mechanisms, and warns against imposing or assuming any one model over another without this detailed understanding (Campbell et al., 2006). The effective deployment of any model would need equally detailed input from all aspects of the social-ecological system.

8.2.3 Grazing impacts and the role of habitat variability

The mosaic of sandy lowland and rocky upland habitats plays an important role in the response of the landscape to sustained heavy grazing. While in some respects these different habitats are a continuation of the vegetation type in which they lie, in other respects they are unique habitats and importantly cannot be viewed as refugia for all plant species in a vegetation type. In terms of understanding the susceptibility of different parts of the landscape to grazing pressure (Vetter, 2005), the vulnerability of the lowland habitats to grazing pressure is highlighted in this study. Measures of change in cover, biomass and plant species composition are more pronounced on these accessible lowland areas and the rocky upland habitats are certainly less heavily grazed. However, the loss of grass on the communal upland habitats may suggests an early sign of grazing induced

compositional change, as discussed previously, and certainly demonstrates that these areas are indeed being grazed to some degree (Chapter 4). It is possible that these upland habitats serve as key resource areas which are used in the dry season or during drought (Illius and O'Connor, 1999). Given the altered state of the lowland habitats on the communal rangeland, these key resource areas would be used more frequently and for longer periods of time on the communal rangeland than on the adjacent private rangeland.

8.2.4 Grazing, ecosystem functioning, conservation and livelihoods

The findings of this study raise concerns for conservation and livelihood sustainability alike. As noted in the introduction, an ecosystem services argument places these two concerns not in opposition but potentially in agreement, where the same end is sought (Diaz et al., 2006), and one need not be given 'privilege' over the other (Benjaminsen et al., 2006). While the sustained heavy grazing on the communal rangeland does not affect plant species richness, it is clearly altering the environment and ecosystem function, evident in compositional and biogeographic shifts where reproductive processes and possibly abiotic environments, for example through increased bare soil, are altered. This is of concern for the conservation of the flora of the area, and equally for livestock keepers where a system is emerging that is highly rainfall-dependent. With climate change predictions pointing to reduced and more erratic rainfall (Rutherford et al., 2000; MacKellar et al., 2007; Midgley and Thuiller, 2007), this will have major implications for livestock keepers in the area. This increase in 'shocks' will undoubtedly render the community of Leliefontein more vulnerable (Vogel and Smith, 2001). There is an apparent need to develop management strategies for these rangelands which meet both agricultural and conservation objectives (Dorrough et al., 2004b), to increase the social and ecological resilience of the area (Walker et al., 2004). Increasingly this is being researched as an option (Bernues et al., 2005), and in some reserves in Australia livestock are now maintained on reserve land and utilized as a management tool (Lunt et al., 2007).

8.2.5 How to best measure grazing impacts

The characterization of the vegetation sampled across the Kamiesberg, presented in Chapter 3, provided an invaluable 'canvas' against which the subsequent grazing

analyses were interpreted. For example where grazing impacts were evident across all the vegetation types, another anticipated grazing response was the homogenization of vegetation types, a grazing impact recorded elsewhere (Hoffman and Cowling, 1990; James et al., 1999). However, this was not evident here, and in the context of the significant abiotic drivers giving rise to distinct vegetation types across the Kamiesberg, this failure to record such a shift is readily explained. Similarly, in the remote sensing analysis it proved extremely useful to have a detailed understanding of the vegetation types where, for example, cover between two vegetation types may be similar, but composition and biomass differ significantly. Without this understanding of the area there would certainly have been scope for misinterpretation. The findings of this study point to a detailed understanding of the biophysical environment as an extremely effective starting point for a grazing ecology study.

The basic growth form analysis adopted in Chapter 4 proved highly effective in elucidating plant community changes in response to grazing. The findings were in keeping with other international studies, lending support to the methodology (Milchunas et al., 1989; Fensham et al., 1999; Hadar et al., 1999). The plant functional type approach presented in Chapter 5 proved disappointing. While this method did bring out some interesting grazing-related impacts, they were not as clear or as universal as those of the growth form analysis. This is attributed to the effects of too coarse an approach in adopting the proposed universal language advocated by plant functional type practitioners (Corelissen et al., 2003). Inappropriate and in some instances too crude a cateogorisation resulted in 'fuzzy' groupings and some grazing responses revealed in Chapter 4 were lost. This study does not support the notion of a universal plant functional type language (Corelissen et al., 2003), but rather suggests the use of site-appropriate measures which should in turn be clearly presented in any published literature to allow for informed comparisons.

The biomass assessment presented in Chapter 6 successfully demonstrated the loss of biomass on the communal rangelands in response to sustained heavy grazing. The use of allometric relationships and generation of volume-biomass curves was effective and

allowed for an assessment of biomass across a large area without excessive amounts of destructive sampling. It is hoped that by publishing the established regression relationships they will be useful in future biomass assessments.

The remote sensing methodology presented in Chapter 7 demonstrated that what is clearly evident from field surveys cannot necessarily be seen in remote sensed imagery. This study would agree with Lillesand (2000) in the suggestion that Landsat imagery be used as a complementary tool, in conjunction with field-based surveys. If used as a stand-alone tool in this study, the communal rangeland might be assumed to show no change in response to sustained heavy grazing, which is certainly not the case. Strong correlations between indices and biomass and cover, however, do show this methodology to have potential.

8.3 INTERVENTIONS, RECOMMENDATIONS AND FUTURE WORK

8.3.1 Scope and context of suggested interventions and recommendations

The sustained heavy grazing associated with high stock numbers on the Leliefontein communal rangeland has made, and continues to make, an impact on the vegetation of the area with consequent concerns for ecosystem functioning and livelihood sustainability. High stock numbers are undoubtedly the primary cause of the recorded landscape alteration. To address this problem, stocking rates on the communal rangelands must be reviewed. While the focus of this study is on vegetation, the author is well aware that the reason people keep stock and the numbers at which they maintain their herds is an issue steeped in social, political, economic and biophysical concerns which go well beyond the realm of this project. In considering appropriate interventions some of these issues are touched on, as they form part of the literature that provides the context for this study, but are only engaged with in respect to the focus of this study.

8.3.2 Consideration of possible interventions and recommendations

Before considering possible interventions, it must be stated that given the findings in this study, the alternative of leaving things as they currently stand is not considered an appropriate option. The recent suggestion that we continue to accept a 'culturally altered' landscape is rejected (Benjaminsen et al., 2006). Aside from complacency around human welfare, where findings in this study point to a trajectory towards increased alteration and exposure to risk, these 'cultural' landscapes are an artefact of an uncomfortable and unjust historical culture that should not be accepted.

However, the enforcement of carrying capacities as a solution is over-simplistic. Forcing livestock keepers to reduce their herd size would have negative economic implications for an already impoverished community. Consequently it is an intervention likely to be met with opposition and such a scheme would have major political and practical obstacles. While social, economic and political concerns are acknowledged, they should not have to compromise good ecological practice, and solutions agreeable to all considerations should be sought. It is argued that other options, aside from the enforcement of conservative stocking regimes, are available and stock numbers can effectively be 'reduced' through other means.

Greater herd mobility is an obvious suggestion in diluting stock numbers across the rangeland. Cowling suggests the 'removal of barriers to stock migration' and the 'nationalisation of the herd' as an ecologically sound approach to stock keeping in the Karoo (Cowling, 1991). Indeed transhumance is practiced as a coping mechanism in arid rangelands (Hesse and Cotula, 2006) and was historically practiced widely in Namaqualand (Smith, 1999; Rohde et al., 2003; Hoffman and Rohde, 2007a), and continues to be today by the wealthier private farmers who frequently own more than one farm (May and Lahiff, 2007). Implementing greater mobility in the context of the communal rangeland, where stock keepers could move livestock seasonally or in response to drought (Hesse and Cotula, 2006), would hinge on national and local political issues around for example, new farm allocation, land tenure security and the strength and capacity of institutional management. In the current climate of contentions around land

tenure issues (Benjaminsen et al., 2006; May and Lahiff, 2007) and apparently weak institutions in the implementation of grazing practices (May, 1997; Jonas, 2004; Lebert and Rohde, 2007; May and Lahiff, 2007), it is unlikely that such an option would prosper at the rangeland scale where it might be effective.

What may be more effective is localised resting of certain areas of the vegetation. The findings of this study, and others (Otto et al., 2006), suggest that this would potentially allow the restoration of certain aspects of ecosystem functioning such as seed set and the successful establishment of perennial plants. This type of rotational resting is described as an effective means of buffering farmers against the potential 'shocks' of variable rainfall (Danckwerts et al., 1993). Areas of rested vegetation would be likely to improve both livelihood concerns with increased reserves of available forage, as well as ecosystem functioning concerns. The development of such a model would need careful consultation between ecologists and livestock farmers in order to derive an optimal and feasible plan. Infrastructure and good institutional support would be pre-requisites. Such a localised approach, which for instance could be implemented in each village in the Leliefontein communal area, would likely mean easier institutional arrangements and more immediately visible benefits.

The removal of feral donkeys from the communal rangeland would see a major reduction in grazing pressure. There are an estimated 4000 donkeys in the Leliefontein communal area (Hoffman et al., 1999). This is included in the estimated total 7 600 large stock units currently grazing the area (Hoffman et al., 1999). At a conversion factor of one donkey as equivalent to 0.65 of a large stock unit, the removal of all the feral donkeys would represent a removal of approximately one third of the grazers in the communal area. This would undoubtedly have significant implications for the recovery of the vegetation of the area. Attempts to remove donkeys in the past have met with local institutional problems (Aggenbag, pers comm.).[4] The need to strengthen local institutions to effectively implement any change is once again highlighted (May, 1997; Wisborg, 2006; Lebert and Rohde, 2007).

[4] Mr Gert Aggenbag is a communal farmer in the Leliefontein area, living in the Klipfontein village.

Another suggestion is that of 'land-sparing' (Balmford et al., 2005), whereby agricultural activities are intensified in certain parts of the landscape while other areas are kept relatively protected (Matson and Vitouset, 2006; Dorrough et al., 2007). There is merit in this idea from a conservation standpoint, where zones are sacrificed and cordoned off areas remain pristine and can be viewed as refugia for plant and animal species. However, this would not address the issue of livelihood security. Furthermore it may serve to enforce a false notion that there are two views in operation in the landscape, one pursuing a livelihood option, and the other pursuing conservation. This polarised view is argued as both unnecessary and counter to the broader objective of landscape level ecosystem functioning and service delivery that benefits both local and wider society (Diaz et al., 2006) and this option is therefore rejected.

A programme of ongoing vegetation restoration is another possible intervention to arrest the erosion of ecosystem functioning and to improve the condition of the rangeland in terms of forage production. This has been shown to be a realistic option in the region, and would have the added benefit of presenting an opportunity for an alternative livelihoods scheme (Anderson et al., 2004). Indeed the provision and diversification of livelihood options is a commonly cited solution to halting alteration as a result of high stock numbers and reducing the degree of risk to livestock farmers (Vetter, 2003; Hesse and Cotula, 2006; Reynolds et al., 2007). Research in the immediate area has shown that the most successful farmers pursue multiple livelihood options in what is termed 'pluriactivity' (Anseeuw and Laurent, 2007).

As suggested by Rohde et al. (2006) issues relating to the communal rangelands of Namaqualand may more likely be resolved through transformation and economic development beyond the communal areas than through an enlightened grazing policy. There is undoubtedly a need for national government to take up the issue of landscape level alteration and the increased threat to livelihood on the communal rangelands. The future of the commonages of Namaqualand must be seen in a national context, where the question of who decides on the use and trajectory of these landscapes must be seen as of

national, or indeed international, interest. It is the role of government to find solutions that address the balance between livelihood opportunities and risk (Stafford Smith and Pickup, 1993). Suggested government interventions in the literature include better access to markets, information and enlightened extension advice, support in building robust local institutions, and livelihood diversification opportunities (Reynolds and Stafford Smith, 2001; Vetter, 2003; Hesse and Cotula, 2006). A further suggestion that would require a national-level approach is that of 'payment for environmental services', where ecosystem services delivered to wider society, for example through services such as carbon sequestration, are measured and given some economic value. On this basis a 'payment for environmental services' model could be implemented, where those members of society benefiting from services generated in rural areas make payments to support the continued delivery of these services (Pagiola et al., 2004). The revenue generated is then used to aid farmers in rural areas who are the custodians of these services, but typically focussed on the private use value (Jackson et al., 2007), in supporting ecologically and economically sustainable practice. It is suggested that this model could stretch as far as the international community, in particular in light of predicted climate change, where the urbanised west could be 'taxed' for their contribution to this form of environmental change (Hesse and Cotula, 2006).

8.3.3 Future research directions

A number of future research directions emerge from this current project. The most significant would be a monitoring study. A re-examination of the vegetation in ten years time would give a better understanding of directional change. Ideally, this would be the monitoring of some intervention, such as a restoration programme or grazing management scheme, which could be measured against this current body of work. Monitoring schemes could engage both the academic and pastoralist communities (Oba and Kotile, 2001; Vetter, 2003). There is scope for the exploration of effective restoration projects, both ecologically and socially. Similarly there is scope for the design and testing of a revised grazing scheme. The transplant experiment gave some interesting insights into differences in species' responses to variable climatic regimes (Chapter 4). Given

predicted environmental change there is scope for more work along these lines in order to inform landscape management decisions in response to change.

The sustained heavy grazing on the Leliefontein communal rangeland has resulted in the area being altered, with evidence of changes in plant community composition, cover and biomass, and biogeographic shifts indicative of alteration. The findings of this ecological research project point to the need for a change in the current farming practices. It is acknowledged that this is a complex matter. This current piece of work has a purely botanical, and within that context, methodological focus, with significant findings to guide and contribute to any future work in this area. However, in considering the results of this research in the context of literature, a major finding must be that in future greater transdisciplinary efforts are required between the social and scientific research communities, and significantly, in conjunction with the community of farmers in the Leliefontein area (Vogel and Smith, 2001; Max-Need, 2005; Jackson et al., 2007).

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